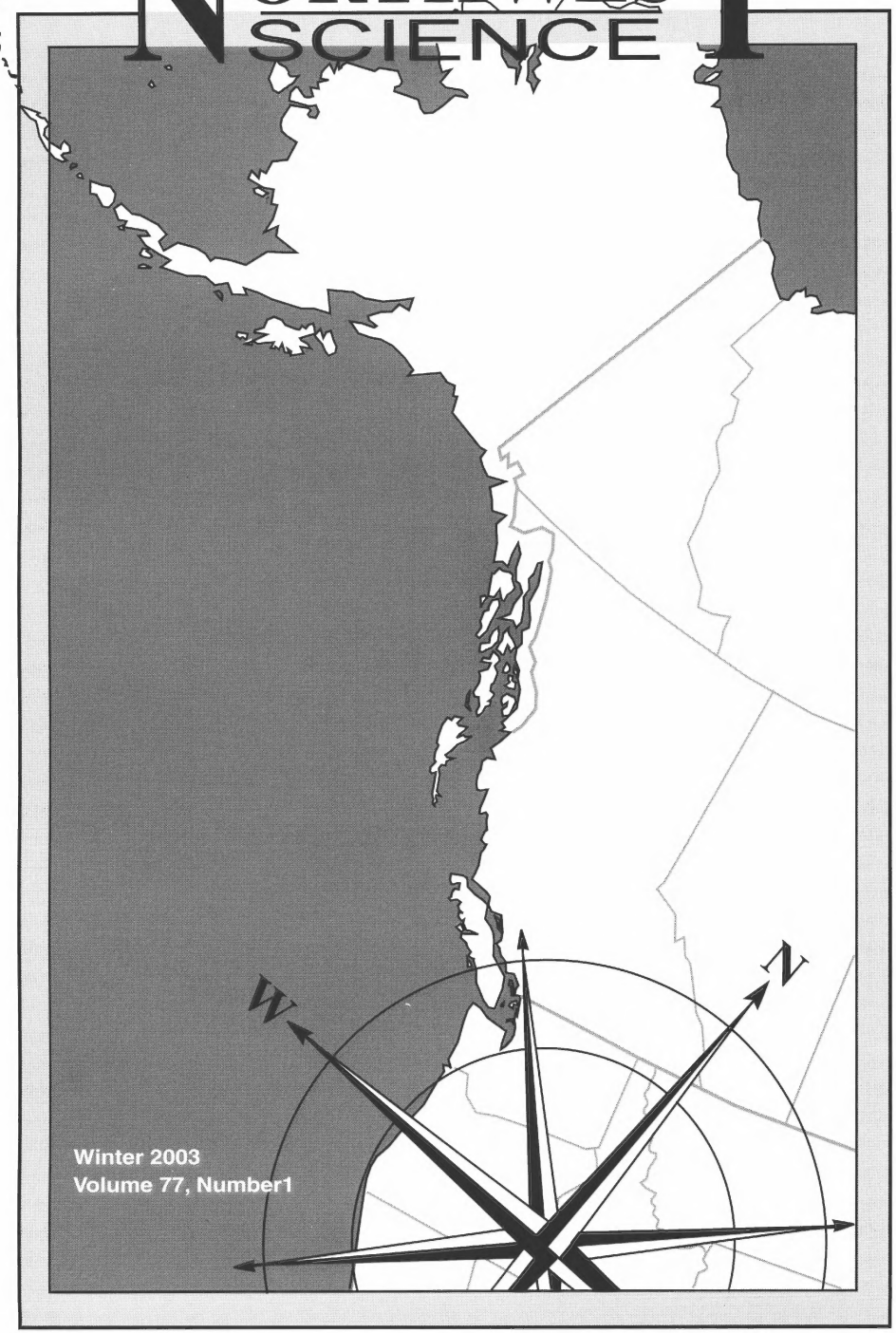
# NORTHWEST SCIENCE

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# Northwest Scientific Association

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# NORTHWEST SCIENCE


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# Announcements

## Erratum to:

Nigh, G.D., P.V. Krestov, and K. Klinka. 2002. Trembling aspen height-age models for British Columbia. Northwest Sci. 76(3):202-212.

Parameter $a_2$ in the denominator of the equation on page 205 is incorrect. It should be -0.9614, not -0.9892. This equation should be:

$$HT = 1.3 + (SI - 1.3) \times \frac{1 + e^{7.423 - 1.150 \times \ln(49.5) - 0.9614 \times \ln(SI - 1.3)}}{1 + e^{7.423 - 1.150 \times \ln(BHA - 0.5) - 0.9614 \times \ln(SI - 1.3)}}$$

## 2003 Annual Meeting, Forks, Washington, 26-29 March

The 76th Annual Meeting of the Northwest Scientific Association will occur at the Olympic Natural Resource Center in Forks, Washington, from Wednesday, 26 March through Saturday, 29 March, 2003. The meeting will be held in conjunction with the Northwest Lichenologists, Oregon white oak working group, USDI National Park Service, USDA National Forest Service, the Washington Department of Natural Resources, and the University of Washington. Field trips are planned for dates before and after the meeting. The major symposium will be on sustainable forestry. Proposed concurrent sessions, symposia, and workshops are scheduled, and both oral presentations and poster presentations are planned.

- Botany session
- Ecology session
- Marine/Aquatic Biology session
- Lichen session
- Zoology session
- Lichen identification workshop
- National vegetation classification discussion group
- Natural areas workshop
- Oregon white oak workshop

Individuals interested in helping to organize sessions or workshops should contact Dan Stephens, Wenatchee Valley College, 1300 Fifth Street, Wenatchee, WA 98801. Phone: 509-664-2503. FAX: 509-664-2538. E-mail: dstephens@wvcmail.ctc.edu.

Registration and accommodation information is available on the NWSA web site, listed on the inside front cover of this issue.

**A. Ross Black,**[1] **George W. Barlow,** and **Allan T. Scholz,** Department of Biology, 258 SCI, Eastern Washington University, 526 5th Street, Cheney, Washington 99004

# Carbon and Nitrogen Stable Isotope Assessment of the Lake Roosevelt Aquatic Food Web

## Abstract

The purpose of this study was to investigate the carbon and nitrogen stable isotope signatures of the common aquatic organisms in Lake Roosevelt, a large volume storage reservoir in the upper Columbia River where annual water level fluctuations limit benthic and littoral productivity and diversity. Carbon isotope signatures were used to indicate the relative importance of benthically versus pelagically fixed carbon in each species diet. Nitrogen isotope signatures were used to identify the trophic level occupied by each species. We expected a limited benthic component in the aquatic community and a need for benthic fishes to use a high proportion of pelagically fixed carbon. Distinct pelagic versus benthic carbon signatures were detected for primary producers and primary consumers (benthic organisms possessed greater $^{13}C$), which meant that the relative importance of the two carbon sources in the diet could be determined. Our collections revealed few benthic organisms, and of those, only one trophic level of benthic consumers was detected from isotope data. Most of the animal diversity in Lake Roosevelt utilizes pelagically fixed carbon. Even those fishes that are usually considered obligate benthivores (cyprinids, catostomids, and cottids) collected more than 65% of their carbon from pelagic sources.

## Introduction

This study investigated the importance and fate of open-water (pelagic) versus near-shore (benthic) primary productivity in the Lake Roosevelt reservoir of the Columbia River, Washington. Our purpose was to track benthic and pelagic carbon flow through the food web to determine the predominant carbon sources for consumers. Stable isotope analysis was chosen for its ability to discern between benthic and pelagic carbon in organism diets (France 1995), and the ability to determine relative trophic status of organisms (DeNiro and Epstein 1981).

Typical lake and reservoir systems have diverse benthic and pelagic communities of primary producers. Fixed carbon arising from both attached benthic algae (periphyton) and planktonic algae (phytoplankton) enters the food web and is passed between consumer level organisms. Lake Roosevelt, Washington, however, undergoes an annual drawdown more extreme than most reservoirs, which effectively eliminates benthic carbon fixation for the duration of the drawdown (Beckman et al. 1985). The reservoir is drawn down an average of 15 m beginning in January and does not return to full pool until mid–July (Nigro et al. 1981). At the peak of the winter drawdown the water level is below the level of the previous summer and autumn euphotic zone, eliminating virtually the entire littoral community of the reservoir. Benthic productivity does not begin until early summer because littoral organisms cannot overwinter in the reservoir, and macrophytic plants and algae that begin to recolonize at the winter low water mark find themselves below the euphotic zone once the water level is returned to normal in July. Significant benthic production may not occur until well into August.

Nearly all fishes in Lake Roosevelt are supported by zooplankton for at least a portion of their lives, usually as juveniles. As adults, these fishes vary between obligate pelagivores, benthivores, or some combination of both. Lake Roosevelt contains several species of fishes that are typically considered in most systems to be obligate benthivores (Wydoski and Whitney 1979, Simpson and Wallace 1982). These include carp (*Cyprinus carpio*), largescale sucker (*Catostomus macrocheilus*), bridgelip sucker (*Catostomus columbianus*), and sculpins (*Cottus* sp.). In a system with limited benthic production, we questioned whether these fishes truly functioned as obligate benthivores, or whether they would be forced to a partially pelagic diet. Stomach content data collected annually from Lake Roosevelt fishes indicated a high benthic diet in these fishes (Peone

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et al. 1991, Griffith and Scholz 1991, Cichosz et al. 1998, Baldwin and Polacek 2002.) However, the majority of the fish collection for stomach analysis occurs in the late summer months when benthic productivity is at its highest, which may give the appearance that fishes are feeding more heavily from the benthic region than they really are. By using stable isotope analysis, we examined food sources over time periods from months to years, which integrated periods of high and low benthic productivity

Benthic carbon entering the food web can be distinguished from pelagic carbon by periphyton's significant enrichment in $\delta^{13}C$ over phytoplankton (France 1995). An organism's stable carbon isotope ratios reflect the isotope ratios of its prey (DeNiro and Epstein 1978) therefore, incorporation of either benthically or pelagically produced carbon can be detected in the $\delta^{13}C$ values of consumers (Keough et al. 1996). Organisms with both benthic and pelagic carbon in their diet will have $\delta^{13}C$ values between those of benthically and pelagically fixed carbon (Peterson and Fry 1987).

Relative trophic status of an organism can be detected by a 3-4‰ increase in $\delta^{15}N$ between prey and predator (DeNiro and Epstein 1981, Minagawa and Wada 1984, Hobson and Welch 1992, Cabana and Rasmussen 1994). With each trophic level increase, a percentage of carbon is lost to feces, metabolism, and specific dynamic activity (Odum 1957). If benthic primary production is minimal in Lake Roosevelt, benthic carbon should become noticeably diminished as carbon is lost from the food web (O'Brien 1990). Depending on food availability, fishes will adjust their diets, in turn altering their stable isotope values (Vander Zanden et. al 1999a). In this case benthically feeding fishes will be forced to a more pelagic diet. The effect that this will have on the isotope ratios of these fishes is that as $\delta^{15}N$ increases, $\delta^{13}C$ should shift toward pelagically derived carbon resulting in relatively lower $\delta^{13}C$ values.

The reservoir's limited littoral productivity, along with the abundance of fishes commonly known to be obligate or facultative benthivores, provides a unique opportunity to study food web structure . This aim of this study was to trace carbon pathways in the reservoir to determine the degree to which benthic and pelagic primary producers were supplying carbon to the food web. We predicted that there would be a complete set of trophic levels of organisms deriving carbon from pelagically based primary producers. In the benthic portion of the food web, however, we predicted that organisms would shift towards a pelagic diet with each increase in trophic level. Thus, as $\delta^{15}N$ increased in benthic organisms, $\delta^{13}C$ was expected to shift towards the pelagic carbon source. If benthic primary productivity is in fact being reduced, stable isotope analysis should show the depletions of benthic carbon in the food web. We hypothesized that fishes that are commonly known to feed partially or exclusively from the benthos would be forced to shift their feeding to encompass a more pelagic diet, resulting in those organisms having stable isotope ratios indicative of a partially pelagic diet.

## Methods

### Study site

Lake Roosevelt is a 243 km long reservoir of the Columbia River, located behind Grande Coulee Dam in northeastern Washington (Figure 1). Grand Coulee Dam was completed in 1939 and reached full pool for the first time in 1941. The reservoir inundates 393 $km^2$ with a storage capacity of 1.16 X $10^{10}$ $m^3$. At a full pool elevation of 397 m above mean sea level the reservoir has a maximum depth of 122 m, and 1544 km of shoreline. The lower portion of the reservoir flows through shrub step, desert terrain, while the middle and upper regions are located in mountainous regions dominated by ponderosa pine (Wilson 1996). Flow through the reservoir has a water residence time that varies from 15 days in the spring to 83 days in the fall and winter. The annual water temperature varies from 2.2°C in the early spring to 20°C in late summer (Weirenga et al. 1997).

The water level of the reservoir is reduced every spring to serve as a recipient of mountain snow melt. The drawdown typically begins in January, peaks sometime in May, and is returned to full pool by the beginning of July. Draw down events, on average, reduce the reservoir's volume by 55%, surface area by 45%, and mean depth by 7 meters (Beckman et al. 1985). The water level is dropped below the euphotic depth eliminating nearly all littoral and benthic primary producers (Beckman et al. 1985). The drawdown levels have averaged 15 m over the past 15 yr, and have varied from a minimum of 4.3 m to the maximum of 25 m (U.S. Army Corps of Engineers 2000). In 1999, however the water level was reduced by 23 m, making

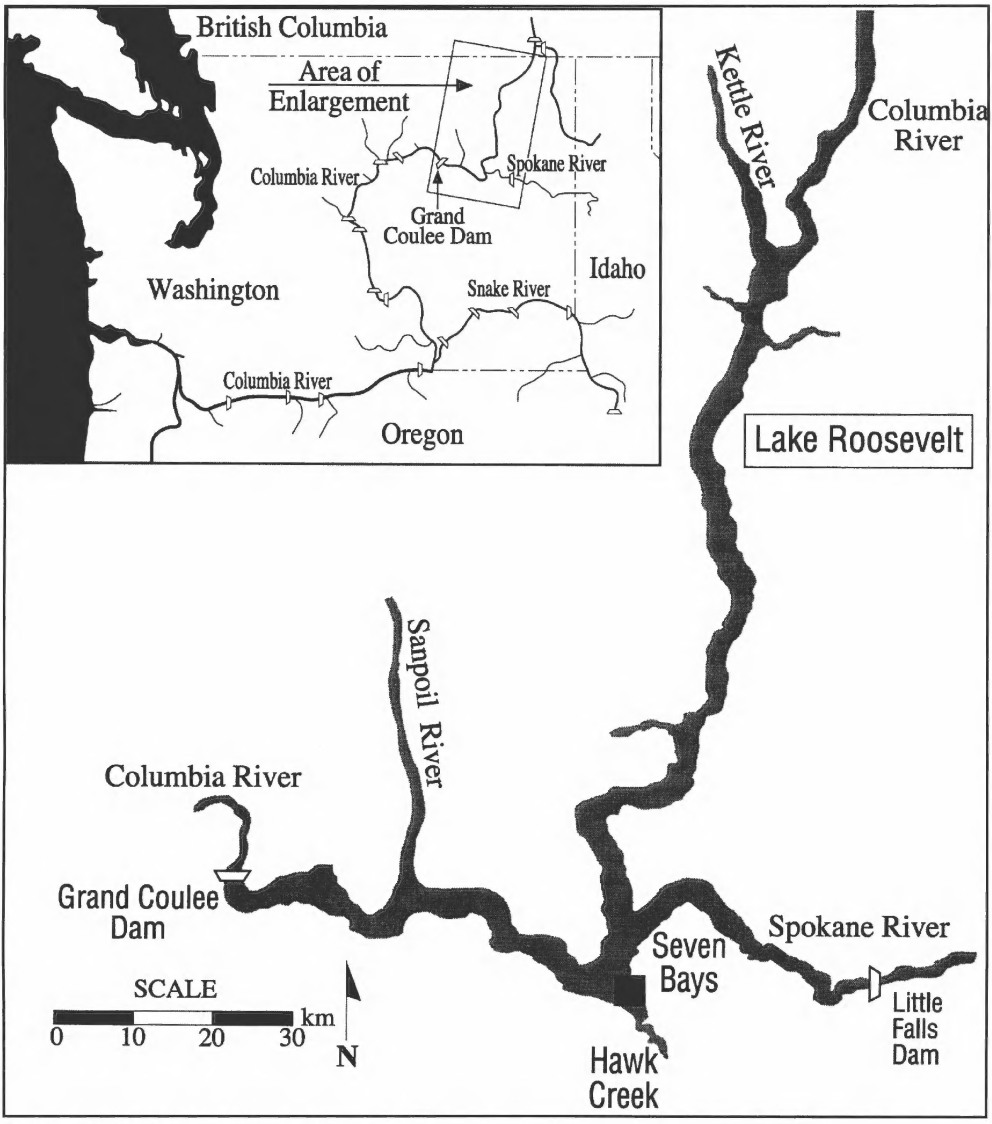


Figure 1. Lake Roosevelt and the collection locations.

it one of the more extreme drawdown events. The 2000 drawdown reduced the reservoir elevation by 17 m making it slightly more extensive than the 15 m average.

All samples were collected from the Seven-Bays and Hawk Creek region of the reservoir (Figure 1). Seven-Bays is named for a series of small bays located on the eastern shoreline. The bays tend to have sandy shorelines that drop off quickly, allowing little benthic primary production. Hawk Creek enters an estuary of Lake Roosevelt after flowing over Hawk Creek Falls, which are impassable to fishes. The estuarine region is left exposed when the reservoir is drawn down, and becomes colonized with reed canary grass. When the reservoir is brought to full pool

the estuary becomes inundated. The inundated reed canary grass (*Phalaris arundinacea*) then provides substrate for periphyton development.

The Seven-Bays and Hawk Creek region of the reservoir was chosen as the study site due to its relatively high species richness and high concentration of fishes. We predicted that the collection of three feeding groups, including obligate benthic feeders, obligate pelagic feeders, and organisms with mixed benthic and pelagic diets would be possible at this location.

## Sample Collection

Samples were collected during the last week of July and the first week of August in 1999 and the first two weeks of August in 2000. Sample collection was limited spatially and temporally to maintain isotopic uniformity. We examined 33 different organisms representative of the Lake Roosevelt food web (Table 1). Phytoplankton were collected from the pelagic region of the reservoir by pumping water from a depth of 1 meter through a 100 µm sieve into 20 L carboys. The majority of the phytoplankton composition consisted of diatoms, with a smaller percentage of green algae and cyanobacteria. The centrifuged phytoplankton pellets were rinsed with deionized water, allowed to resettle, and dried for 24 hr at 60°C.

Periphyton were collected from two locations in the reservoir. A dip net was used to collect periphyton colonizing submerged reed canary grass in the Hawk Creek arm, and in the Seven Bays region it was scraped from substrate suspended at a depth between 1 and 2 m in the open water. The periphyton were rinsed repeatedly with deionized water at the lab to remove colonized invertebrates.

Zooplankton were collected from the pelagic region by vertical hauls with a 0.5 m diameter, 200 µm mesh, conical plankton net. Species were isolated and concentrated using a combination of sieving and hand picking. Chironomids were collected from the sediment and from submerged reed canary grass. An Eckman dredge was used to collect chironomids from the sediment, and a dip net was used to collect them from the reed grass beds, along with corixids, aquatic mites, and snails. Invertebrates were grouped together by taxa and collection site, rinsed with deionized water, dried at 60°C for 24 hr, ground to homogeneity, and sealed in glass vials. Each individual invertebrate sample was composed of enough individuals to ensure dry mass exceeded five mg.

Fishes were collected with electroshocking boats, backpack electroshocking gear, and vertical and horizontal gill nets. The majority of the adult fishes were collected with the electroshocking boats, while the majority of the young-of-the-year (YOY) fishes were collected with backpack gear. The gill nets were used predominantly to catch lake whitefish (*Coregonus clupeaformes*), kokanee (*Oncorhyncus nerka*) and burbot (*Lota lota*).

A section of dorsal muscle tissue was filleted from each fish for analysis. Fishes too small to be filleted had their heads and viscera removed in preparation for analysis. All samples were rinsed with deionized water, dried at 60°C, ground to homogeneity, and stored in glass vials.

## Stable Isotope Ratio Analysis

Carbon and nitrogen stable isotope ratios were analyzed by the Stable Isotope Ratio Facility for Ecological Research (SIRFER) at the University of Utah. Samples collected in each year were pooled and single, multi-year averages (±1 SE) were calculated for $\delta^{13}C$ and $\delta^{15}N$ for each taxon. Increases in $\delta^{15}N$ values were considered increases in trophic status. There is a typical increase in $\delta^{15}N$ of 3‰ (DeNiro and Epstein 1981) and $\delta^{13}C$ of 1‰ (DeNiro and Epstein 1978) between predator and prey, resulting in a mean slope of three for trophic level increases when the $\delta$ values are plotted. Organisms that fell within these parameters were considered to be obtaining similar levels of benthic or pelagic carbon.

The proportion of pelagic carbon utilized by each taxa was estimated by plotting a line with a slope of 3 through the primary consumer for each of the benthic and pelagic components of the food web on the $\delta^{13}C$ and $\delta^{15}N$ plane (as per Vander Zanden et al. 1999a and Post 2002). The pelagic and benthic primary producers were not used because seasonal variation makes them an unreliable base for a food chain plot (Zohary et al. 1994). *Daphnia* were used as the pelagic primary consumer and snails were used as the benthic primary consumer. The proportion of pelagic carbon utilized by each species was then estimated from the relative horizontal position occupied by each species between the pelagic and benthic lines. The trophic level occupied by each organism was calculated as per Hobson and Welch (1995) and

TABLE 1. Mean and standard error (SE) for $\delta^{13}C$ and $\delta^{15}N$ for each of the sample taxa. Sample sizes are included for each year of collection. Trophic level was calculated as per the equation of Hobson and Welch (1995) and using the $\delta^{15}N$ values of *Daphnia* as the pelagic primary consumer upon which all other trophic level calculations were based. Percent pelagic represents an estimate of the proportional abundance of pelagic carbon in each organisms diet (see text for calculation methods).

| Sample | Abbrev. | n 1999 | n 2000 | $\delta^{13}C$ Mean (SE) | $\delta^{15}N$ Mean (SE) | Trophic Level | % Pelagic |
|---|---|---|---|---|---|---|---|
| Bryozoan | BR | 0 | 1 | -29.10 (0.00) | 2.50 (0.00) | 1.5 | 85 |
| Sponge | SP | 0 | 5 | -29.28 (0.02) | 2.82 (0.08) | 1.6 | 82 |
| *Sida crystallina* | SC | 3 | 6 | -28.93 (0.39) | 3.56 (0.25) | 1.8 | 84 |
| Periphyton | PE | 11 | 19 | -22.75 (0.39) | 4.16 (0.30) | 2 | 0 |
| Phytoplankton | PH | 6 | 17 | -28.36 (0.32) | 4.18 (0.19) | 2 | 100 |
| *Daphnia* sp. | DA | 10 | 14 | -30.16 (0.35) | 4.25 (0.27) | 2 | 100 |
| *Leptodiaptomus ashlandi* | LA | 0 | 2 | -29.20 (0.20) | 5.15 (0.05) | 2.3 | 100 |
| Zooplankton | ZP | 4 | 0 | -30.23 (0.08) | 5.65 (0.22) | 2.4 | 100 |
| *Epischura nevadensis* | EN | 1 | 7 | -30.41 (0.77) | 5.76 (0.06) | 2.4 | 100 |
| Snails | SN | 4 | 0 | -20.83 (0.49) | 5.80 (0.21) | 2.5 | 0 |
| *Diacyclops thomasi* | DT | 0 | 1 | -29.20 (0.00) | 5.80 (0.00) | 2.5 | 100 |
| Copepod | CP | 6 | 0 | -30.10 (0.10) | 7.03 (0.12) | 2.8 | 100 |
| Chironomidae | CH | 11 | 12 | -25.21 (0.61) | 7.31 (0.23) | 2.9 | 56 |
| *Leptodora kindti* | LK | 5 | 4 | -30.28 (0.18) | 7.49 (0.36) | 3 | 100 |
| Corixidae | CO | 3 | 3 | -26.03 (012) | 7.65 (0.37) | 3 | 67 |
| Smallmouth bass (YOY) *Micropterus dolomieui* | SB | 3 | 0 | -26.47 (0.17) | 7.70 (0.12) | 3 | 72 |
| Aquatic Mites | AM | 3 | 1 | -26.70 (0.29) | 9.13 (0.58) | 3.4 | 79 |
| Yellow perch (YOY) *Perca flavescens* | YPj | 6 | 12 | -27.39 (0.23) | 9.33 (0.29) | 3.5 | 88 |
| Rainbow trout (Hatchery) *Oncorhynchus mykiss* | RTh | 4 | 7 | -25.44 (0.49) | 9.84 (0.17) | 3.6 | 67 |
| Bridgelip sucker *Catostomus columbianus* | BS | 0 | 2 | -27.75 (0.35) | 10.00 (0.60) | 3.7 | 94 |
| Carp *Cyprinus carpio* | CA | 9 | 9 | -25.34 (0.33) | 10.23 (0.14) | 3.8 | 68 |
| Brook trout *Salvelinus fontinalis* | BT | 4 | 3 | -26.54 (0.67) | 10.33 (0.43) | 3.8 | 82 |
| Kokanee (wild) *Oncorhynchus nerka* | KOw | 3 | 3 | -28.73 (0.23) | 10.42 (0.23) | 3.8 | 100 |
| Rainbow trout (wild) | RTw | 8 | 24 | -26.35 (0.41) | 10.43 (0.19) | 3.8 | 80 |
| Largescale sucker *Catostomus macrocheilus* | LS | 7 | 12 | -25.25 (0.08) | 10.58 (0.03) | 3.9 | 68 |
| Whitefish *Coregonus clupeaformis* | WF | 9 | 11 | -29.09 (0.14) | 10.61 (0.21) | 3.9 | 100 |
| Smallmouth bass *Micropterus dolomieui* | SB | 5 | 17 | 25.79 (0.16) | 10.85 (0.16) | 3.9 | 76 |
| Northern pikeminnow *Ptychocheilus oregonensis* | NP | 3 | 9 | -26.39 (0.36) | 10.85 (0.31) | 3.9 | 82 |
| Sculpin (Cottidae) | SU | 10 | 10 | -25.81 (0.21) | 10.97 (0.12) | 4 | 77 |
| Yellow perch (adult) | YP | 7 | 12 | -27.23 (0.18) | 11.38 (0.34) | 4.1 | 93 |
| Kokanee (hatchery) | KOh | 3 | 7 | -25.40 (0.05) | 11.50 (0.07) | 4.1 | 73 |
| Walleye *Stizostedion vitruem* | WA | 10 | 33 | -26.13 (0.11) | 12.00 (0.15) | 4.3 | 84 |
| Burbot *Lota lota* | BU | 4 | 13 | -27.92 (0.08) | 12.24 (0.14) | 4.4 | 100 |

used the $\delta^{15}N$ value for *Daphnia* as the primary consumer in the food chain.

## Results

Mean (and SE) $\delta^{13}C$ and $\delta^{15}N$ values, and the estimated trophic position, for each of the 33 taxa included in this study are presented from lowest to highest trophic position in Table 1. The position of each taxa on the $\delta^{13}C$ and $\delta^{15}N$ plane is presented in Figure 2. The most important result for the purposes of this study was periphyton were considerably more enriched in $^{13}C$ than phytoplankton (–22.8 $\delta^{13}C$ versus –28.4 $\delta^{13}C$), which allowed us to distinguish benthic from pelagic food components of the food web (Figure 2). Given one can make this distinction among primary producers, and given food chain constituents are arranged on the $\delta^{13}C$ and $\delta^{15}N$ plane along a line with slope of approximately 3 (DeNiro and Epstein 1981), there is a striking lack of exclusively benthic consumers in the Lake Roosevelt food web. Snails were the only organisms that our results identified as exclusive consumers of benthically fixed carbon (Figure 2). Although their position in Figure 2 suggests heavy utilization of pelagic carbon, chironomids appear to rely upon benthic carbon sources for 44% of their diet. All other taxa, especially higher trophic level organisms, appear to collect the majority of their carbon from pelagically fixed sources (Figure 2).

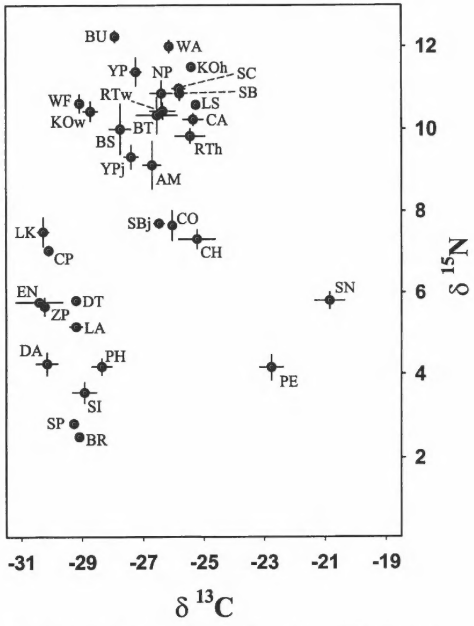


Figure 2. Stable isotope ratios for carbon ($\delta^{13}C$, ‰) and nitrogen ($\delta^{15}N$, ‰) for the food web components of Lake Roosevelt for 1999 and 2000. Table 1 provides a key to species abbreviations.

The Lake Roosevelt aquatic community contains a rich pelagic component. The water flea *Daphnia* (including *D. schodleri*, *D. galeata*, *D. retrocurva*), and additional branchiopod *Sida crystallina*, and the calanoid copepod *Leptodiaptomus ashlandi*, were the pelagic herbivores that were abundant during the collection period. Their trophic level positions were estimated at 2.0, 1.8, and 2.3 (Table 1). The herbivorous branchiopod *Bosmina longirostris* may also be common in Lake Roosevelt, but abundances were too low during collection periods to permit inclusion in the study. Potentially predacious zooplankters included the calanoid copepod *Epischura nevadensis*, the cyclopoid copepod *Diacyclops thomasi*, and the large branchiopod *Leptodora kindti*. *Epischura* and *Diacyclops* both exhibited omnivorous diets with trophic level estimates that were approximately one-half trophic level above *Daphnia* (Table 1). The trophic level estimate for Leptodora was 3 (one full trophic level above *Daphnia*) and suggests an exclusively predacious diet and reliance upon *Daphnia* as a prey item. The pelagic vertebrate planktivores included wild kokanee (*Oncorhynchus nerka*) and lake whitefish (*Coregonus clupeaformis*). Their estimated trophic levels (3.8 and 3.9) suggest they primarily consume the larger predatory species of zooplankton. Burbot was observed as the top trophic level consumer, with the highest $\delta^{15}N$ value of any lake Roosevelt consumer (Figure 2), and 3.4 trophic levels above *Daphnia* (Table 1). The position of the exclusively pelagic animals in Figure 2 illustrates a linear structure with a slope of 2.6 ($P$=0.035) that spans more than two trophic levels. When examined by year, the pelagic taxa had a linear structure with a slope of 2.4 in 1999 ($P$= 0.004), and a slope of 3.4 in 2000 ($P$=0.011).

All other organisms included in this study exhibit increased $\delta^{13}C$ and $\delta^{15}N$ suggesting at least partial inclusion of benthic carbon in their diet and increased trophic status when compared to the pelagic invertebrates. Existing at approximately the same trophic level as *Leptodora* were YOY smallmouth bass (*Micropterus dolomieui*), corixids, and chironomids (Figure 2), with chironomids

exhibiting a smaller portion of benthic carbon in their diet than either YOY smallmouth bass or corixids (Table 1). Aquatic mites held the highest trophic position among the invertebrate organisms (trophic level = 3.4): the relative importance of pelagic carbon in their diet was estimated at 79%. Young-of-the-year yellow perch occupied a trophic position similar to the aquatic mites (Figure 2) and pelagic carbon was estimated to comprise 88% of their diet (Table 1).

The majority of the fishes in Lake Roosevelt occupied fairly high trophic position (trophic level ≥ 3.6) and primarily utilize pelagic carbon (Table 1, Figure 2). Bridgelip sucker (*Catostomus columbianus*), carp (*Cyprinus carpio*), brook trout (*Salvelinus fontinalis*), kokanee (*Oncorhynchus nerka*), rainbow trout (*Oncorhynchus mykiss*), largescale sucker (*Catostomus macrocheilus*), whitefish (*Coregonus clupeaformis*), smallmouth bass, and northern pikeminnow (*Ptychocheilus oregonensis*) all possessed trophic level estimates between 3.6 and 3.9 (Table 1). Among these, kokanee and whitefish exhibited the largest utilization of pelagic carbon, and largescale sucker the least (Table 1). Those fishes observed to occupy the highest trophic positions in Lake Roosevelt included sculpins (*Cottus* sp.), yellow perch (*Perca flavescens*), walleye (*Stizostedion vitreum*), and burbot (*Lota lota*). Trophic position among these fishes ranged from 4 to 4.4, and utilization of pelagic carbon ranged from 77% (for *Cottus*) to 100% for burbot (Table 1).

Our estimates of the dietary contribution of pelagic carbon (Table 1) illustrate exceptionally little utilization of benthic carbon in Lake Roosevelt. Snails were the only organisms that appeared to rely exclusively on benthic carbon. All others appear to collect the majority of their carbon from pelagic sources. Chironomids exhibited the least utilization of pelagic carbon. Among the fishes, estimated consumption of pelagic carbon ranged from 68% to 100%. And for those fishes assumed to feed within the benthic portion of the food web ( sculpin, carp, suckers) the lowest estimated proportion of pelagic carbon in the diet was 68% for carp and largescale sucker. Among the fishes listed above, the pelagic contribution to the diet averaged 77%, and was as high as 94% (for bridgelip sucker).

Although we fully expected to observe little benthic carbon utilization among the Lake Roosevelt organisms, a few unusual results are noteworthy. We were surprised to see *Daphnia* and phytoplankton possessing identical $\delta^{15}N$ values suggesting they occupy similar trophic position (Figure 2). We were also surprised to observe sponges, bryozoans, and *Sida* with $\delta^{15}N$ values that were below the $\delta^{15}N$ values of phytoplankton (Figure 2). Additionally, if snails consume only periphyton, their $\delta^{15}N$ values should be enriched by approximately 3‰ over periphyton (Deniro and Epstein 1981). These anomalies may be a result of primary producers giving unreliable or questionable isotope signatures (Zohary et al.1994). Both Vander Zanden et al. (1999a) and Post (2002) identify problems with primary producer isotope signatures and recommend using benthic and pelagic primary consumers as the base of their respective food chains when examining trophic relationships among higher trophic level organisms. Finally, there is no relationship whatsoever between the isotope signature of hatchery reared and wild salmonids. For both kokanee and rainbow trout, those of hatchery origin were more enriched in $^{13}C$, and their estimated trophic level varied from the wild fish (Table 1, Figure 2).

## Discussion

The first objective of this study was to determine the feasibility of C and N stable isotope analysis for observing the food web structure of Lake Roosevelt. Periphyton were significantly more enriched in $^{13}C$ than phytoplankton (Figure 2), which allowed us to distinguish between the two carbon pathways. The $\delta^{15}N$ values showed uniform stepwise enrichment in relation to the trophic status of organisms, especially in the pelagic portion of the food web (Figure 2). Together, the two isotope ratios indicate a system with a strong pelagic component and a diminutive benthic component in the aquatic food web. Lake Roosevelt supports a well defined pelagic component in the food web that consists of multiple trophic levels (Figure 2). Nitrogen isotopes demonstrated herbivorous, omnivorous, and carnivorous zooplankton (Table 1). The planktonic invertebrates provided the diet for wild kokanee and lake whitefish, and these fishes provided the primary prey source for burbot (Figure 2). Because there are organisms with exclusively pelagic diets having $\delta^{15}N$ values ranging from the lowest consumer to the top predator, we believe there is an adequate supply of pelagically fixed carbon in the reservoir. Given several species of benthic fishes are present in

Lake Roosevelt, if there were an adequate supply of benthically fixed carbon, there should have been organisms with exclusively benthic carbon signatures from the primary producer through the top consumer trophic level. However, the exclusively benthic component of the food web never extended beyond the primary consumer level (Figure 2). The stepwise shift away from a benthic diet and toward a pelagic diet with each trophic increase suggests that minimal levels of benthic carbon are fixed in the reservoir. The benthic carbon that is lost to metabolism and excretion with each trophic increase is replaced with the abundant pelagically fixed carbon, leaving a void in the food web plots in the region where higher level benthic consumers would be expected to be positioned by stable isotope theory (Figure 2).

Of the fishes typically considered to be obligate benthivores, all had isotope values indicating pelagic carbon in their diet (Table 1). Our most extreme example was bridgelip sucker, which had $\delta^{13}C$ values indicating 94% utilization of pelagic carbon. The degree to which the benthic fishes consumed benthically produced carbon varied, but it did not appear to make up more than 32% of the diet for any of them. Those fishes that were predicted to have an exclusively benthic diet did have carbon signatures indicating the highest reliance upon benthically produced carbon of any fishes in the reservoir (with the exception of hatchery fishes), yet the majority of their carbon intake was still from pelagic production. The reason for this is that there simply appears to be little benthic carbon in the overall Lake Roosevelt food web. Snails were the only organisms to have carbon signatures indicating an exclusively benthic diet (Figure 2). Stomach data collected from Lake Roosevelt by others has indicated all fishes have at least low levels of zooplankton in their diet (Baldwin and Polacek 2002). During our collection periods, largescale suckers and carp were witnessed swimming in the reservoir just below the surface, feeding on the abundant zooplankton. Since 1997 we have routinely observed largescale suckers feeding on the surface throughout the reservoir on nearly every occasion that we sampled fish (39–87 days per year). This suggests many fishes may adjust their feeding habits when their natural food source is not available.

Conflicting information exists between stomach content data and isotope data. Isotope data indicated that burbot were feeding primarily on the planktivorous fishes, kokanee and lake whitefish (Figure 2). However, stomach data presented in Cichosz et al. (1998) indicates burbot diets do not include salmonids. Stomach samples had been collected primarily during late summer when the reservoir has returned to full pool. It is quite likely that the stomach data represent the snapshot in time phenomena where one receives a view of what the fish has eaten in the past few hours, but that is not necessarily representative of the overall majority of its diet. Burbot move into the shallows in the fall, at the same time kokanee move into the stream mouths to spawn. Burbot are suspected of preying heavily on kokanee at this time and we have collected several burbot with kokanee in their stomachs at these locations, which further conflicts with stomach data (Cichosz et al. 1998).

It was difficult to determine exactly what walleye were feeding on from the isotope data. According to their isotope ratios they could have been feeding on a combination of several fishes (Figure 2), which agrees with 1998 stomach data (Spotts et al. 2000) in which walleye had been observed to prey upon members of several fish families present in the reservoir. Although, no salmonids were found in walleye stomachs from the individuals collected for this study, walleye are thought to prey heavily on kokanee and trout in the reservoir (Baldwin and Polacek, 2002). We have pumped many kokanee and rainbows out of Lake Roosevelt walleye stomachs using lavage techniques. In some cases, individual walleye contained as many as 12 kokanee or rainbow trout.

Existing stomach content data suggest kokanee and lake whitefish had a 93% diet overlap in 1997 (Cichosz et al. 1998), which correlates well with isotope data (Figure 2). Cichosz et al. (1998) also report 91% diet overlap between kokanee and rainbow trout and a diet consisting of both pelagic and benthic prey. However, our isotope data indicate a much greater difference, and no benthic component in kokanee diets (Figure 2). Wild rainbow trout had $\delta^{13}C$ values that indicate their diets are composed of approximately 80% benthic prey (Table 1). This discrepancy, as with the one mentioned above for burbot, is perhaps an artifact of the stomach samples having been collected when benthic productivity is at its annual peak and the stomach contents only represent the organisms diet over the previous several hours. The stable isotope data conversely provide a long-term average

of the seasonal variation in the organisms diet. Here, it is likely the stomach data exaggerate the importance of benthic prey in kokanee diets.

The northern pikeminnow isotopic data placed it in the secondary consumer, mixed diet group which is lower than was predicted. The northern pikeminnow was once common in Lake Roosevelt and constituted up to 60% of the total gillnet catch in 1948 (Gangmark and Fulton 1949). However, the northern pikeminnow population has been steadily declining, with a gillnet relative abundance of 26% in 1965 (Earnest et al. 1966), 15% from 1980–1983 (Beckman et al. 1985), 6% in 1990 (Griffith and Scholz 1991), and <1% in 1996 (Cichosz et al. 1998). In the lower Columbia River system northern pikeminnow prey heavily on juvenile salmon and steelhead (Zimmerman and Ward 1999). The decline in the northern pikeminnow population in Lake Roosevelt has mirrored the rise in population of the introduced walleye, which was not recorded in gillnet catches until 1965. The walleye population increased to 29% of the relative abundance by 1980–1982 (Beckman et al. 1985), and has since leveled off in the range of 15–25% between 1988 and the present (Peone et al. 1991, Griffith and Scholz 1991, Cichosz et al. 1998). Vander Zanden et al. (1999b) used stable isotopes to examine trophic changes in aquatic food webs with the invasion of a competing predator. Lake trout in lakes with introduced smallmouth bass had more negative $\delta^{13}C$ values (–29.2‰ versus –27.4‰) and reduced trophic status (3.3 versus 3.9). The $\delta^{13}C$ values indicated a shift away from a diet of mostly fish to a diet of mostly zooplankton. The decrease in trophic status as determined from $\delta^{15}N$ values further indicates a shift to a zooplankton diet. Vander Zanden et al. (1999b) suggest that when bass are introduced to a lake system, they outcompete lake trout for forage fish, forcing the trout to a diet consisting primarily of zooplankton. The highly predacious nature of walleye (Francis and Vondracek 1990) may allow them to displace the northern pikeminnow. Northern pikeminnow diets typically consist of fish and benthic invertebrates (Wydoski and Whitney 1979, Simpson and Wallace 1982). If walleye outcompete pikeminnow for a fish-based diet, as indicated by $\delta^{15}N$ values, the pikeminnow is forced to rely more heavily on benthic invertebrates. The strongest competition between the two would most likely occur in the spring, prior to the arrival of a new crop of YOY forage fishes. Northern pikeminnow would be forced to a diet consisting of their other prey item, benthic invertebrates. At the same time, however, benthic invertebrates are in short supply due to the drawdown. Isotope data have also suggest there is not enough benthic carbon to support secondary consumers, which may help explain the decline in the northern pikeminnow.

It is apparent that stable isotope analysis is sufficient for tracing broad carbon pathways in Lake Roosevelt, providing a view of the reservoir's overall food web structure. The high number of fishes in the mixed benthic-pelagic feeding group made it difficult to trace precise carbon pathways. To determine precisely what these fishes are feeding on, one would have to include stomach data. Stomach data will provide precise information on what an organism has eaten at one point in time, but as we have suggested, there can be conflicts between isotope data and stomach data taken from only one point in the year. Isotope data, coupled with stomach content data collected from several sample dates through the year would give the most precise view of carbon pathways in an ecosystem. Perhaps more importantly, although many of the large western storage reservoirs possess a diverse assemblage of what are considered benthic and pelagic fishes, our results suggest these aquatic systems are driven by pelagic carbon. Resource managers should be made aware of the detrimental impact water level fluctuations can have on the benthic component of aquatic food webs. Thus, in systems similar to Lake Roosevelt, those environmental factors which affect open water productivity are likely to impact the entire food web.

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## Literature Cited

Baldwin, C., and M. Polacek. 2002. Evaluation of limiting factors for stocked kokanee and rainbow trout in Lake Roosevelt. Unpublished annual report submitted to Spokane Tribe of Indians, Lake Roosevelt Fisheries Evaluation Program, Wellpinit, WA. Contract No. 94BI32148. Washington Department of Fish and Wildlife, Spokane, Washington.

Beckman, L. G., J. F. Novotny, W. R. Parsons, and T. T. Tarrel. 1985. Assessment of the fisheries and limnology in Lake F. D. Roosevelt 1980-1983. U. S. Fish and Wildlife Service. Unpublished final report to U. S. Bureau of Reclamation. Contract No. WPRS-0-07-10-X0216;FWS-1406-009-904. Seattle, Washington.

Cabana, G., and J. B. Rasmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372:255-257.

Cichosz, T.A., J. P. Sheilds, K.D. Underwood, A. T. Scholz, and M. B. Tilson. 1998. Lake Roosevelt fisheries and limnological research: 1996 unpublished annual report. U.S. Department of Energy, Bonneville Power Administration. Report No. DOE/BP-32148-2. Portland, Oregon.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution on carbon isotopes in animals. Geochimica Et Cosmochimica Acta 42:496-506.

DeNiro, M. J., and S. Epstein. 1981. Influence of diet on the distribution on nitrogen isotopes in animals. Geochimica Et Cosmochimica Acta 45:341-351.

Earnest, D. E., M. H. Spence, R. W. Kiser, and W. D. Brunson. 1966. A survey of the fish populations, zooplankton, bottom fauna, and some physical characteristics of Roosevelt Lake: unpublished research report. Washington Department of Fish and Game, Fisheries Management Division, Olympia, Wahington.

France, R. L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series 124:307-312.

Francis, J. T., and Vondracek, B. 1990. Predator prey interactions of Lake Erie walleye: 1 July 1987–30 June 1990. Unpublished final report. Ohio Department of Natural Resources, Division of Wildlife. Columbus, Ohio

Gangmark, H. A., and L. A. Fulton. 1949. Preliminary surveys of Lake Roosevelt in relation to game fishes. U.S. Fish and Wildlife Service Special Science Report No. 5. Seattle, Washington.

Griffith, J. R., and Scholz, A. T. 1991. Lake Roosevelt fisheries monitoring program: Annual report 1990. Prepared for: Fred Holm, Project manager. U.S. Department of Energy. Bonneville Power Administration. Report No. DOE/BP-19819-3. Portland, Oregon.

Hobson, K. A., and H. E. Welch. 1992. Determination of trophic relations within a high arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K. A., and H. E. Welch. 1995. Cannibalism and trophic structure in a high arctic lake: insights from stable isotope analysis. Canadian Journal of Fisheries and Aquatic Sciences. 52:1195-1201.

Keough, J. M., M. Sierszen, and C. A. Hagley. 1996. Analysis of a Lake Superior coastal food web with stable isotope techniques. Limnology and Oceanography 41:1135-1140.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of $^{15}N$ along food chains; further evidence and relation between $\delta^{15}N$ and animal age. Geochimica Et Cosmochimica Acta 48:1135-1140.

Nigro, A. A., T. T. Terrel, and T. G. Beckman. 1981. Assessment of the limnology and fisheries in F. D. Roosevelt Reservoir. Unpublished annual report. Prepared for the U.S. Bureau of Reclamation, by the U. S. Fish and Wildlife Service, National Fishery Research Center, Seattle, Washington.

O'Brien, W. J. 1990. Perspectives on fish in reservoir ecosystems. Pages 209-226 *in* K. W. Thornton, B. L. Kimmel, and F. E. Payne, editors, Reservoir Limnology. John Wiley and Sons, New York.

Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27:55-112.

Peone, T. L, A. T. Scholz, J. R. Griffith, S. Graves, and M. G. Thatcher. 1991. Lake Roosevelt fisheries monitoring program: unpublished annual report, 1989. U.S. Department of Energy, Bonneville Power Administration, Report No. DOE/BP-91819-1. Portland, Oregon.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Simpson, J. C., and R. L. Wallace. 1982. Fishes of Idaho. University of Idaho Press, Moscow, Idaho.

Spotts, J. V., J. P. Shields, T. C. Cichosz, and K. D. Underwood. 2000. Unpublished annual report,1998. Lake Roosevelt fisheries monitoring and evaluation program creel survey and population analysis. Spokane Tribe of Indians. Department of Natural Resources. Prepared for the Bonneville Power Administration. Division of Fish and Wildlife. Portland, Oregon.

U.S. Army Corps of Engineers. 2000. Water Management Division. Available online at www.NWD-WC.usace.army.mil/TMT/tdg-data/months.html

Vander Zanden, M. J., B. J. Shuter, N. Lester, and J. B. Rassmussen. 1999a. Patterns of food chain length in lakes: A stable isotope study. American Naturalist 154:406-416.

Vander Zanden, M. J., J. M., Casselman, and J. B. Rassmussen. 1999b. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464-467.

Weirenga, R. E., S. T. J. Juul, and W. H. Funk. 1997. Investigation into the primary productivity of Lake Roosevelt, Washington. Unpublished interim report. State of Washington Water Research Center, Pullman, Washington.

Wilson, G. A. 1996. Nutrient and trophic state reduction in the Franklin D. Roosevelt Reservoir of Washington State. State of Washington Water Research Center, Pullman, Washington.

Wydoski, R. S, and R. R. Whitney. 1979. Inland Fishes of Washington. University of Washington Press, Seattle, Washington.

Zimmerman, M. P., and D. L. Ward. 1999. Index of predation on juvenile salmonids by northern pikeminnow in the lower Columbia River basin, 1994–1996. Transactions of the American Fisheries Society 128:995-1007.

Zohary, T., J. Erez, M. Gophen. 1994. Seasonality of stable carbon isotopes within the pelagic food web of Lake Kinneret. Limnology and Oceanography 39:1030-1043.

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# Grylloblattids in Managed Forests of South-central British Columbia

## Abstract

We collected 147 specimens of grylloblattids (*Grylloblatta campodeiformis*) in pitfall traps in subalpine spruce-fir forest and lower elevation cedar-hemlock forest at two study sites in south-central British Columbia. Grylloblattids are of conservation interest because of the high degree of endemism in western North America and because little is known of the ecology of these insects. Mature grylloblattid individuals were caught primarily in early spring or late fall, while immature individuals were caught in traps set under the snow in winter. Grylloblattids occurred in clearcuts, partial cuts and uncut forest at both sites. Year-round collections of grylloblattids from a variety of forest habitats have not previously been reported. However, the insects were rare at one study site in old clearcuts and had different seasonal patterns of captures in recent clearcuts with intensive site preparation compared to partially-cut or uncut areas. At a second study site, they showed an affinity for cutblock edges and small patch cut harvest treatments that produce abundant edge. No grylloblattids were collected during similar sampling at a third site in dry Douglas-fir forest. The unexpected abundance of grylloblattids at two sites suggests that they may be widespread in wetter forest sites, but dry forests with low snowfall may act as a geographic barrier. Grylloblattids appear to tolerate or benefit from forest harvesting, other than in large clearcuts with intensive site preparation.

## Introduction

Notoptera is one of the rarest and least-known insect orders, comprising two genera in Asia and one genus, *Grylloblatta*, found only in western North America (Rentz 1982). One species of grylloblattid, *Grylloblatta campodeiformis,* has been found in the Rocky Mountains in Canada and the northern United States, in isolated locations in northern British Columbia and along the Thompson River drainage in south-central British Columbia (Kamp 1979). At least nine other species in the genus *Grylloblatta* occur in apparently relict populations in the Coast and Cascade Mountains from southwestern British Columbia to northern California (Rentz 1982). Kamp (1979) attributed the geographic distribution of species in this genus to isolation of the coastal species in glacial refugia during the Pleistocene.

Grylloblattids are cold-adapted (Ford 1926, Mills and Pepper 1937, Kamp 1973), with a preferred temperature at high relative humidity of –3.5°C to +5°C, and optimal temperature of +1.7°C (Henson 1957a, Kamp 1973). Due to these narrow microclimatic preferences, this species is often thought to occur primarily in high-elevation areas near snow-fields or glaciers that provide cold, moist conditions throughout the year (Ford 1926, Kamp 1973, Edwards 1982). Grylloblattids are closely associated with the alpine or subalpine hypolithion, the layer in or under rock fields, where crevices provide suitable micro-climates in extreme summer and winter conditions (Kamp 1973, 1979). Presence at moderate elevations is associated with extensive rockpiles and cooling by subsurface flows of melt water (Kamp 1973, Pritchard and Scholefield 1978, Edwards 1982). Further corroborating the idea that grylloblattids require special habitat features to meet their narrow micro-climate preferences, one exceptional population at low elevation in a semi-desert environment near Kamloops, British Columbia, was restricted to a deep talus slope. This habitat feature allowed access to ground temperatures near freezing year-round, despite mid-summer air temperatures >40°C (Campbell 1949). The rarity and patchy nature of apparently suitable habitat types led Kamp (1979) to postulate that North American grylloblattids occurred in highly disjunct distributions, with local populations largely isolated by unsuitable habitat.

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In northern coniferous forests, however, numerous features other than permanent ice and snow fields or talus slopes can provide moist microhabitats with low temperatures in summer, including deep moss layers, large logs, and dense vegetation cover. In winter, deep snowpacks can insulate the ground surface and maintain moist, near-freezing conditions throughout the area. We report the collection of numerous grylloblattids at two forest sites in south-central British Columbia, which demonstrate that the habitat requirements and distribution of this species of grylloblattid may not be as restrictive as previously believed. Because forest management affects ground microclimate and snow accumulation (Golding 1982, Chen et al. 1995) and alters some of the forest characteristics that could provide suitable microhabitats for grylloblattids, such as the moss layer (Stokland 1991) and coarse woody debris (Harmon et al. 1986), conservation of this rare order could be a concern in managed forests. Our primary objective was to document the distribution of grylloblattids in forest habitats and to provide an assessment of the possible effects of forest management on this species. We used a retrospective treatment design at one study site and large-scale experimental manipulations at a second site for this purpose. We also report results from a third study area in dry Douglas-fir forest, for our secondary objective of improving understanding of the biogeography of the genus.

## Methods

### Study sites

The East Barriere Lake (EBL) study site is located south of East Barriere Lake, 75 km northeast of Kamloops, British Columbia. Elevations in the 6 km x 8 km study area range from 1000 m in the valley bottoms to 1750 m on the tops of ridges. Forests below 1350 m are in the Interior Cedar-Hemlock (ICH) biogeoclimatic zone, and above 1350 m in the Engelmann spruce–subalpine fir (ESSF) zone (Lloyd et al. 1990). The ICH is considered interior temperate rain forest, with a closed canopy forest of western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*) and other conifers, and a variety of early seral deciduous species (Lloyd et al. 1990). The ESSF zone is subalpine forest with a more open canopy of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), and white-flowered rhododendron (*Rhododendron albiflorum*) as the dominant shrub species (Lloyd et al. 1990). The alpine areas nearest to the site are 25 km to the north and 32 km to the east. A deep snowpack is present from mid-October until June in the ESSF zone, and from late-October until May in the ICH. Summers are generally cool and wet. Forests have been harvested in the area for 40 yr.

The EBL study used three replicate cutblocks or stands of the following seven treatments:

1. ESSF uncut forest. These stands are all > 140 yr old.

2. ESSF partial cut. Approximately 50% of the timber volume was removed from these stands 15–25 yr before the study, with an emphasis on harvesting Engelmann spruce and larger subalpine fir. Coarse woody debris and shrub cover are abundant on these sites.

3. ESSF clearcut. All trees on these blocks were removed 15–20 yr before the study. The sites were burned, mechanically scarified, and planted with Engelmann spruce. The planted trees are < 1.5 m tall, the sites are dominated by annual herbs, and coarse woody debris is scarce.

4. ICH uncut. Two of the three study stands are old-growth redcedar and hemlock (> 250 yr old); the other is natural second-growth Douglas-fir and redcedar (130 yr old).

5. ICH partial cut. 20–50% of the timber volume was removed from these sites 20–35 yr before the study, with an emphasis on harvesting western white pine (*Pinus monticola*) and Engelmann spruce. These sites are at the upper elevation limit of ICH, where preferred tree species occurred. The sites have wide, herb- and shrub-dominated logging trails interspersed with thick deciduous and conifer regeneration under the canopy conifers.

6. ICH old clearcut. All trees on these sites were removed 15–25 yr ago, and the sites were burned and planted. Regeneration is dominated by deciduous species and shrub cover is tall and dense.

7. ICH recent clearcut. These sites were harvested 2–5 yr prior to the start of the study, then burned and planted. Regenerating conifers are < 1.5 m tall and the sites are dominated by annual herbs.

The Sicamous Creek (SC) site is an experimental silvicultural systems site in ESSF forest, located 8 km southeast of Sicamous, British Columbia (Vyse 1999). The site is north-facing, at elevations between 1550 m and 1800 m. A deep snowpack is present from late September until late June; summers are cool and wet. The site was unlogged old forest until winter 1994-95, when five experimental harvest treatments were applied: 1. Single 10-ha clearcut, 2. Array of nine 1-ha patch cuts, 3. Array of fifty-five 0.1-ha patch cuts, 4. Individual tree selection cut, 5. Uncut control. Three replicates of each treatment were applied in a randomized block design to fifteen 30-ha experimental units. With associated roads and landings, each of the four harvest treatments removed 33% of the trees in a unit. In addition to the five overall treatments, the experiment created four harvest types: 1. Clearcut—within the 10-ha, 1-ha or 0.1-ha openings > 10 m from the forest edge, 2. Edge—within 5 m of the edge of the clearcut opening and the forest, 3. Partial cut—within the individual-tree selection harvests, 4. Uncut—in either the uncut control blocks or >10 m from an opening in the forested leave strips of the patch-cut or clearcut treatment blocks.

The Opax Mountain (OM) study area is also an experimental silvicultural systems site, in the Interior Douglas-fir zone (IDF) (Lloyd et al. 1990), 15 km northwest of Kamloops, British Columbia. The site is dominated by Douglas-fir, with a pinegrass (*Calamagrostis rubescens*) understory, on varied topography of volcanic origin. Summers are hot and dry; winters are cold with relatively little snow accumulation and frequent freezing of the ground down to the mineral soil. Experimental harvest treatments in twelve 20-ha units at the site created a range of forest conditions, including 1.6-ha and smaller patch cuts, 50% and 20% removal partial cuts, uncut stands, and leave strips.

## Sampling Design

We sampled ground-dwelling invertebrates using pitfall traps consisting of 400-ml smooth plastic beverage cups with 9.5 cm diameter top set flush with the ground surface. A 30 x 30 cm board held on stakes 15 cm above each trap kept out rain and debris. For summer trapping, 5 pitfall traps were arranged in a trap circle of 7 m diameter. Three trap circles, 50-75 m apart, were used to subsample each replicate block at EBL and SC, for a total of 15 pitfall traps per replicate block. In 1996, an additional set of three circles was added to each block at SC, for a total of 30 pitfall traps per block. Two sets of five circles were used in each replicate block at OM. For winter trapping, each circle had one pitfall trap under a 1.2 m tall plywood chimney supported 10 cm above the cup on a 60 x 60 cm base board. Chimneys were 30 x 30 cm, with a plywood lid, and 5-cm thick foam insulation at three levels. In 1993/94, we increased winter trapping effort to three chimneys per trap circle at EBL and SC. Some of the additional winter traps at SC used 10 cm diameter plastic pipes to form chimneys, also insulated with foam. Temperature probes with automatic readings throughout the day and night showed that the ground temperature under both types of chimneys and under undisturbed snowpack remained near 0°C from December to May.

Pitfall traps were set by adding 100 ml of a mixture of 35% water and 65% propylene glycol, a non-volatile antifreeze, to the pitfall cup. In snow-free seasons, samples were collected after 2 wk, the glycol was replenished and a second sample was collected 2 wk later. In winter, the traps were set in early January through the chimney without disturbing the snow cover and collected 2 mo later. All grylloblattids in the samples were removed from the samples. Body length was measured from the front of the head to the base of the cerci using an ocular micrometer. Individuals ≥10 mm in length were considered mature or submature; individuals <10 mm in length were considered immature. Fully mature individuals with external genitalia and darkened exoskeletons were between 13 mm and 16 mm long.

Samples were collected at EBL in June (1994–1996), July (1994), August–September (1991–1995), October (1994–1995), and winter (1992/93–1995/96). Samples were collected at SC in July (1996–1997), August (1992–1997), and winter (1993/94 and 1995/96–1996/97). Harvesting at SC occurred in winter 1994/95. Samples at OM were collected in: May–June (1995–1997), July–August (1994–1996), September–October (1993, 1995–1996), and winter (1994/95–1996/97). For seasonal summaries, 2-wk sessions in May or June were considered spring, sessions in July or August were considered summer, and sessions in September or October were considered autumn.

TABLE 1. Trapping effort, number of grylloblattids collected, and body lengths at the East Barriere Lake (EBL) and Sicamous Creek (SC) study sites. Immatures are defined as individuals with body length <10 mm.

| Site | Season | Trap-days | Grylloblatid specimens | | Length (mm) | | % Immature |
|---|---|---|---|---|---|---|---|
| | | | Number | per 10,000 trap-days | Mean | SD | |
| EBL | Spring | 15,484 | 14 | 9.0 | 13.6 | 2.2 | 0.0 |
| | Summer | 36,526 | 4 | 1.1 | 14.9 | 1.2 | 0.0 |
| | Autumn | 21,420 | 19 | 8.9 | 12.9 | 3.0 | 0.0 |
| | Winter | 36,152 | 41 | 11.3 | 6.3 | 2.2 | 95.1 |
| SC | Summer | 64,358 | 20 | 3.1 | 15.0 | 0.9 | 5.0 |
| | Winter | 33,166 | 49 | 14.8 | 6.7 | 3.6 | 84.4 |

Statistical tests of treatment effects at EBL used a single-factor ANOVA. Tests of overall treatment effects and effects of finer-scale harvest types at SC used a randomized block ANOVA. A significance level of 0.05 was used.

## Results

We collected 78 grylloblattids in 109,582 pitfall trap-days at EBL. Four adult males from EBL have been identified as *Grylloblatta campodeiformis campodeiformis* (Vernon R. Vickery, Lyman Museum, McGill University, Montreal, Quebec, personal communication). Grylloblattids at EBL were collected primarily in winter, in spring just after snowmelt, or in fall just prior to snowfall (Table 1). Few were collected in summer, despite high levels of trapping effort in that season.

Grylloblattids were found in 18 of the 21 replicate blocks across the EBL site, including open rocky clearcuts, thick brushy sites, and mossy old-growth forest at low and high elevations. The three blocks where grylloblattids were not found had no obvious common features and included one open ESSF partial cut, one rocky ESSF clearcut, and one old ICH clear cut with dense vegetation. Grylloblattids were present in all treatment types, but the temporal pattern of captures differed between the ICH and ESSF sites, with many ESSF captures in snow-free seasons and most ICH captures in the winter under the snowpack (Figure 1). Grylloblattid abundance in snow-free seasons generally increased with elevation, being high in ESSF sites, moderate in the ICH partial cuts at middle elevations and lowest in the other ICH sites at lower elevations, even though treatment differences were not statistically significant in these seasons. Abundance in winter did differ significantly between treatments (Figure 1), without any apparent relationship to elevation or snow depth and duration.

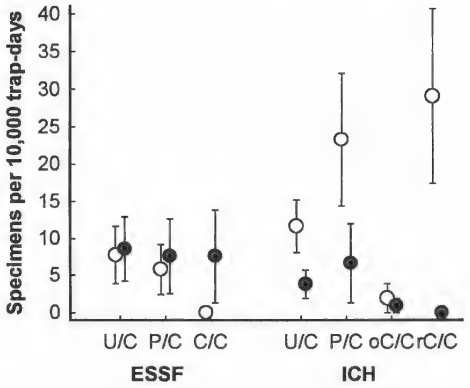


Figure 1. Grylloblattids captured per 10,000 pitfall trap-days in summer (closed circles) and winter (open circles) in seven treatments at EBL. ESSF = Engelmann spruce–subalpine fir forest, ICH = Interior cedar–hemlock forest, U/C = uncut, P/C = partial cut, C/C = clearcut, oC/C = old clearcut, rC/C = recent clearcut. Error bars are 1 S.E.

Individuals collected in winter at EBL were generally small and immature, while individuals collected from spring through fall were larger submature or mature (Table 1). The low standard deviation of body lengths (Table 1) demonstrates the limited range of body sizes collected in each season. The difference in size is a seasonal effect. It is not due to ICH individuals dominating winter samples and ESSF individuals dominating snow-free samples, because all seven winter specimens from ESSF were also immature, and 9 of 13 ICH specimens from snow-free seasons were mature or submature.

Grylloblattid captures per 10,000 trap-days at SC in summer and winter were similar to the values for those seasons at EBL (Table 1). Immature individuals similarly dominated winter samples and all but one summer specimen was mature or submature. Grylloblattids were present in all study blocks across the relatively homogeneous SC site, and were found in all treatment types and harvest types after logging. Catch of grylloblattids per unit effort in winter was the same in pre-harvest forest and post-harvest clearcuts and uncut forest, while partial cuts had somewhat fewer grylloblattids (Figure 2). Grylloblattid abundance was significantly higher on the edges of clearcuts,

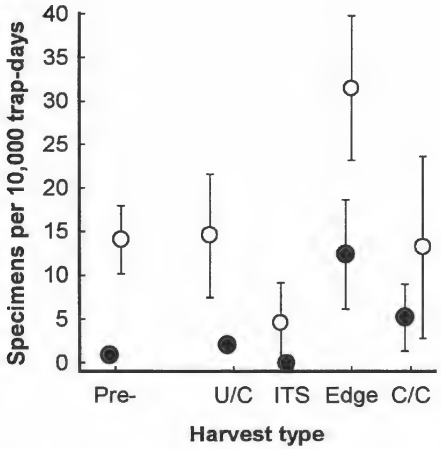


Figure 2. Grylloblattids captured per 10,000 pitfall trap-days in summer (closed circles) and winter (open circles) at SC by harvest type. Pre- = uncut forest prior to harvesting, U/C = uncut controls and leave strips, ITS = individual-tree selection partial cut, Edge = within 5 m of clearcut-forest edge, C/C = clearcut sites in 0.1-ha, 1-ha or 10-ha openings. Error bars are 1 S.E.

in both summer and winter (Figure 2). Correspondingly, catch per unit effort tended to be higher in the 0.1-ha patch cut array treatment, which has large amounts of edge, although overall treatment effects were highly variable and not statistically significant (Figure 3).

No grylloblattids were collected at OM in 13,594 trap-days in spring, 22,008 trap-days in summer, 26,572 trap-days in autumn or 34,328 trap-days in winter.

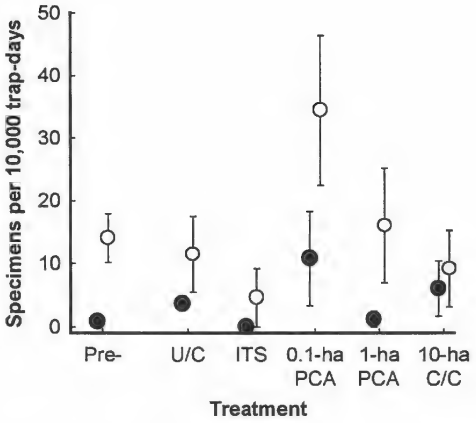


Figure 3. Grylloblattids captured per 10,000 pitfall trap-days in summer (closed circles) and winter (open circles) at SC by overall treatment. Pre- = uncut forest prior to harvesting, U/C = uncut controls, ITS = individual-tree selection partial cuts. The patch-cut arrays (PCA) and 10-ha clearcut (C/C) treatments include the openings and uncut leave strips. Error bars are 1 S.E.

## Discussion

This study is the first to report year-round occurrence of grylloblattids in a wide variety of forested habitats. The ubiquity of grylloblattids at the East Barriere Lake and the Sicamous Creek sites, and even their presence there, was not expected from previous reports of their restrictive habitat preferences and patchy distribution. However, the results from these two study areas are likely not ecological anomalies. Instead, we believe that the unexpectedly large collections of grylloblattids are due to the use of pitfall traps throughout the year. Pitfall traps have rarely been used to sample arthropods in higher-elevation forests in western North America, particularly in winter. Previous collections of grylloblattids have relied on active searching, during which collectors tend to concentrate on habitats and locations thought to be favorable for the species (Ford 1926, Kamp 1973), perhaps falsely indicating a restricted habitat tolerance and distribution. Active searching would be unlikely to find grylloblattids inhabiting forest floor materials, and would not detect activity under the snow. Future studies of this group should use pitfall traps, particularly in winter, early spring, and late fall.

The dominance of small individuals in winter samples and large, mature individuals in snow-free samples indicates different seasonal activity patterns for the two groups, rather than indicating the phenology of the species, because grylloblattids are known to remain in juvenile stages and to live as adults for several years (Henson 1957b). The stable microclimatic conditions under snow and reduced activity of predaceous arthropods may be more favorable to small grylloblattids than conditions at snowfree times, while the larger adults may be less sensitive to variable microclimates and increased predators in snowfree periods. However, this explanation does not account for the rarity of adults in winter samples.

Several conditions could make the dry Douglas-fir forest, represented by the OM site, unsuitable for grylloblattids. Summers are hot and dry, with shallow soils and solid bedrock providing few opportunities for cool refugia. Large well-decayed coarse woody debris is rare, due to frequent fires. Low winter temperatures without a deep insulating snowpack allow the ground to freeze, eliminating the moist, near-freezing subnivean spaces found in ICH and ESSF forests. IDF forests, and even drier habitat types, extend south from central British Columbia through the British Columbia Interior, expanding into the Great Basin of the western United States. This band of habitat that is currently unsuitable for grylloblattids may provide an alternative or complementary mechanism to Kamp's (1979) Pleistocene glacial explanation of the isolation of west-coast grylloblattid species from *G. campodeiformis* in the Rocky and Selkirk mountain areas. If these dry, low-snowfall ecosystems are important dispersal barriers for grylloblattids, undiscovered populations could be expected in isolated areas with wetter forests and deeper snowpacks within the Great Basin and its extension into British Columbia.

Grylloblattids were originally discovered in western Canada, and half of the approximately 20 species currently recognized in the order are endemic to western North America (Rentz 1982). With a high degree of endemism, the order should be an important conservation concern where it occurs in western North America. Previous portrayal of the group's typical habitat as isolated alpine areas, rock, snow fields, and ice caves suggested that forest management was not a conservation issue for grylloblattids. However, we have shown that grylloblattids are forest-dwelling species in at least two common forest types in British Columbia.

In this study, grylloblattids tolerated a wide range of managed forest conditions, but there was some indication that they are affected by harvesting that uses large clearcuts and intensive site preparation. In ESSF forest at EBL, grylloblattids in snow-free seasons (mature and submature individuals) were found in similar abundance in uncut, partially cut, and clearcut forests, but no winter specimens (immature individuals) were collected in ESSF clearcuts. In contrast, the recent ICH clearcuts had many immature individuals but lacked mature adults, while uncut and partial cut ICH forest had both mature and immature individuals. Old ICH clearcuts had few of either age class. The absence of grylloblattids in clearcuts in one season or the other suggests that clearcuts with intensive site disturbance cannot maintain all life stages of the species, warranting concern about the effects of harvesting on these insects.

In the ESSF forest at the experimental SC site, there was no difference in abundances of grylloblattids, including mature and immature animals, between clearcut areas, uncut controls, or pre-harvest uncut forest. In contrast to EBL, clearcuts at SC have not been burned or subject to intensive site preparation. Additionally, the relatively high abundance of grylloblattids along cutblock edges suggests that they may benefit from the abundant edge created by small openings. The increasing operational use of alternatives to large clearcuts and less severe site preparation should help to ensure the conservation of this unique insect species in managed forests.

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## Literature Cited


Campbell, M. G. 1949. Notes on *Grylloblatta* at Kamloops. Entomological Society of British Columbia 45:1-5.

Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. Ecological Applications 5:74-86.

Edwards, J. S. 1982. Habitat, behavior and neurobiology of an American grylloblattid. Pages 19-28 *In* H. Ando (editor), Biology of the Notoptera, Kashiyo-Insatsu Co. Ltd., Nagano, Japan.

Ford, N. 1926. On the behavior of *Grylloblatta.* Canadian Entomologist 58:66-70.

Golding, D.L. 1982. Snow accumulation patterns in openings and adjacent forest. Canadian Hydrological Symposium 82:91-112.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Henson, W. R. 1957a. Temperature preference of *Grylloblatta campodeiformis* Walker. Nature 179:637.

Henson, W. R. 1957b. Notes on a collection of *Grylloblatta campodeiformis* Walker. Canadian Field-Naturalist 71:149-152.

Kamp, J. W. 1973. Biosystematics of the Grylloblattodea. Ph. D. Dissertation, University of British Columbia, Vancouver, British Columbia.



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Kamp, J. W. 1979. Taxonomy, distribution, and zoogeographic evolution of *Grylloblatta* in Canada (Insecta:Notoptera). Canadian Entomologist 111:27-38.

Lloyd, D., K. Angove, G. Hope, and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. Land Management Handbook 23. British Columbia Ministry of Forests, Victoria, British Columbia.

Mills, H. B., and J. H. Pepper. 1937. Observations on *Grylloblatta campodeiformis* Walker. Annals of the Entomological Society of America 30:269-274.

Pritchard, G., and P. Scholefield. 1978. Observations on the food, feeding behaviour, and associated sense organs of *Grylloblatta campodeiformis* (Grylloblattodea). Canadian Entomologist 110:205-212.

Rentz, D. C. F. 1982. A review of the systematics, distribution and bionomics of the North American Grylloblattidae. Pages 1-18 *In* H. Ando (editor), Biology of the Notoptera, Kashiyo-Insatsu Co. Ltd., Nagano, Japan.

Stokland, J. N. 1991. The impact of modern forestry on endangered species in the boreal forest. Fauna (Oslo) 44:11-19.

Vyse, A. 1999. Is everything all right up there? A long term interdisciplinary silvicultural systems project in a high-elevation fir-spruce forest at Sicamous Creek. Forestry Chronicles 75:467-472.

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# Diet Composition of Northern Pikeminnow in the Lower Granite Reservoir System

## Abstract

Predation in Columbia River basin reservoirs by northern pikeminnow can be a major source of mortality of juvenile anadromous salmonids near dams. The purpose of this project was to estimate the diet composition of northern pikeminnow in the tailrace and forebay of Lower Granite Dam, Snake River, and compare with those from the more lotic habitat in upper Lower Granite Reservoir. Crustaceans and nonsalmonid fishes were the most abundant food items by weight in stomach samples collected from northern pikeminnow from April through August 1996 and 1997. Juvenile salmonids were not a major component of northern pikeminnow diets at any sampling locations as we found juvenile salmonid remains in 0.5% of 396 northern pikeminnow stomachs examined. Our results suggest that slamonid predation may be reduced relative to earlier years when lower flows occurred.

## Introduction

Returns of wild Snake River salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss)* have declined dramatically from historic levels. Currently, all remaining species of wild Snake River salmon are listed as endangered or threatened, and wild steelhead are listed as threatened by the National Marine Fisheries Service under the Endangered Species Act of 1973 (National Marine Fisheries Service 1992). Dams have transformed the once riverine environment into a series of slackwater pools. Snake River stocks of juvenile anadromous salmonids pass as many as eight mainstem dams during their seaward migration. As a result, mortality rates of juvenile salmonids have increased because of passage through turbines, increased migration times, asynchronous smoltification, and gas bubble disease from nitrogen saturation (Raymond 1968, Bently and Raymond 1976, Ebel and Raymond 1976, Rosentreter 1977, Weitkamp and Katz 1980, Zaugg et al. 1985). Predation also has been implicated as a major source of mortality of juvenile salmonids (Rieman et al. 1991).

Fish predators annually consumed an estimated 2.7 million juvenile salmonids that entered John Day Reservoir, Columbia River, from 1983 to 1986 (Rieman et al. 1991). Northern pikeminnow (*Ptychocheilus oregonensis)* were responsible for 78% of the estimated loss. Predation rates were the highest in the McNary Dam tailrace where northern pikeminnow were estimated to be 12 to 18 times more abundant than in other parts of the reservoir (Beamesderfer and Rieman 1991). Although predation was especially intense in the McNary Dam tailrace, juvenile salmonids composed more than 60% of northern pikeminnow diets in the John Day Dam forebay (Poe et al. 1991). Reiman and Beamesderfer (1990) reported that sustained exploitation of northern pikeminnow longer than 275 mm could substantially reduce predation on juvenile salmonids. In 1991 the Sport Reward Program (SRP) was initiated to pay anglers for removal of northern pikeminnow from the Columbia and Snake rivers.

Management of piscivorous fishes in the Columbia River basin has been based largely on recent studies at John Day Reservoir, however some evidence suggests predator-prey relations may be quite different in the lower Snake River reservoirs (Ward et al. 1995). Ward et al. (1995) found that predation of juvenile salmonids by northern pikeminnow was much higher in the lower Columbia River than in middle Columbia or lower Snake rivers. The purpose of our study was to assess diet composition of northern pikeminnow in the Lower Granite Reservoir system.

## Study Area

Lower Granite Reservoir is located in southeastern Washington and west central Idaho near the cities of Clarkston, Washington, and Lewiston, Idaho (Figure 1). Lower Granite Dam was completed

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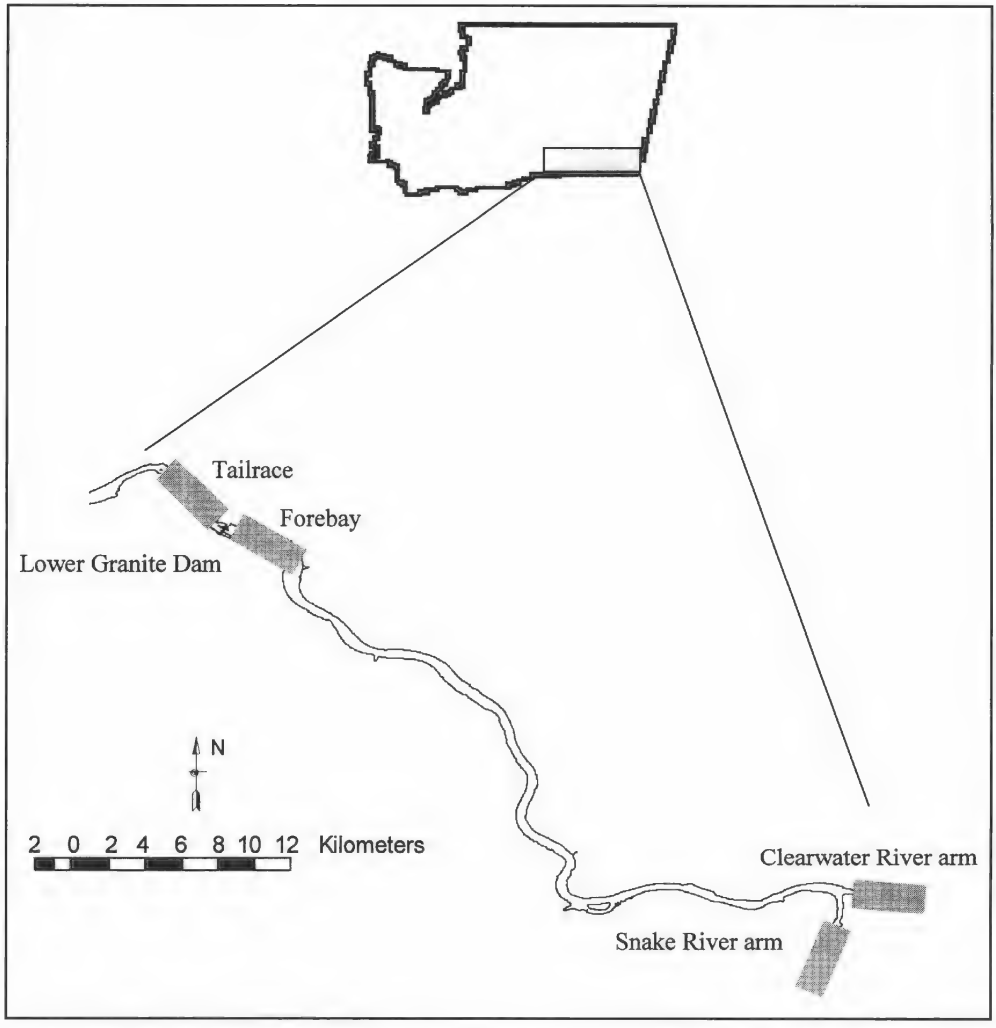


Figure 1. Sampling locations in the Lower Granite Reservoir and tailrace from April through August 1996 and 1997.

in 1975 to provide hydroelectric power, barge navigation, recreation, and flood control (Bennett et al. 1983).

Lower Granite Reservoir has a total surface area of 3,602 ha at full pool, a mean depth of 16.6 m, a maximum depth of 42.1 m (Curet 1993), and extends from Lower Granite Dam (river kilometer (rkm) 173.1) upstream beyond the confluence of the Snake and Clearwater rivers in Idaho. Surface water temperatures typically range from <7°C in March to 25°C in late summer (Funk et al. 1985). Shoreline habitat consists of rip-rap, cobble, talus, sand-silt beaches, and embayments (Bennett et al. 1983).

We selected four main locations in our study area to capture the range of physical variation in reservoir habitat: the tailrace (rkm 167-173), the forebay (rkm 173-179), the Snake River arm (rkm 225-238), and the Clearwater River arm (rkm 0-6). Locations in the forebay and tailrace included the restriction zones (RZ) immediately adjacent to Lower Granite Dam.

Three species of juvenile anadromous salmonids migrate through Lower Granite Reservoir: chinook salmon (*O. tshawytscha*), steelhead, and sockeye salmon (*O. nerka*). Spring and summer chinook salmon, steelhead, and sockeye salmon juveniles migrate seaward in April, May, and June as yearlings or older fish. Fall chinook salmon migrate seaward in June, July, and August as subyearlings (Connor et al. 1998). In 1996, nearly eight million juvenile salmonids were collected at Lower Granite Dam, whereas nearly seven million fish were collected in 1997. Juvenile salmonid migrations at Lower Granite Dam in 1996 and 1997 were made up of 9% spring or summer chinook salmon, 90% steelhead, and <1% sockeye and fall chinook salmon (Fish Passage Center 1996, 1997).

## Methods

### Northern Pikeminnow Collections

We collected northern pikeminnow near and parallel to the shoreline in the four sampling locations by using nighttime electrofishing with an output of 400 volts at 3-5 amps. Sampling was conducted to coincide with peak feeding activity of northern pikeminnow that occurs at dawn and dusk (Steinberger and Larkin 1974, Vigg et al. 1991). We used proportional allocation methods (Scheaffer et al. 1990) to determine the number of sites of each habitat to sample within each reservoir location. Each week, we sampled at least eight, 400-m sites in the tailrace and forebay from April-August 1996 and 1997, 16 sites from May-August in the Snake River Arm in 1996 (eight sites from April-August in 1997), and eight sites from May-August in the Clearwater River Arm in both years.

All northern pikeminnow collected were immediately placed in a live well and measured for total length (mm). Weights of captured fish were estimated using weight-length regressions developed by Bennett et al. (1983). Northern pikeminnow ≥200 mm, the approximate minimum size of salmonid predators (Poe et al. 1991, Chandler 1993), were killed for stomach analysis.

### Prey Collections and Dietary Analysis

We removed the entire digestive tract because northern pikeminnow lack a true stomach (Hofer 1991). Stomach contents were collected by cutting open the body cavity, pinching shut the anterior end of the esophagus behind the pharyngeal teeth, and stripping the contents into a plastic cup. Within each site in the field, all collections were preserved in a 10% buffered formalin solution.

In the laboratory, prey items were identified with the aid of a dissecting microscope and divided into the following prey groups: macroinvertebrates, crustaceans, nonsalmonids and salmonids. Each prey group was blotted dry and weighed to the nearest 0.0001 g. Partially digested, unidentifiable macroinvertebrates were weighed as a group. When prey fish were too digested to measure fork or total length, diagnostic bone lengths (Hansel et al. 1988) and nape to tail lengths (Vigg et al. 1991) were used to estimate the fork length using regression equations. Diagnostic bone lengths were taken from cleithra, opercles, pharyngeal teeth, and dentaries found in stomachs of northern pikeminnow. Vertebrae shape was used to distinguish between salmonid and nonsalmonid prey fish when other diagnostic bones were absent. We pooled salmonid prey into a general category of salmonids because stock identification was not possible.

## Results

We examined the stomach contents of 396 of 648 northern pikeminnow collected in 1996 and 1997. The remaining fish were released with tags in an attempt to estimate their abundance or implanted with radio-transmitters (Piaskowski 1998). In 1996, 106 (81%) of the northern pikeminnow stomachs examined were from fish <349 mm in length, whereas 25 were from northern pikeminnow >349 mm in length. We sampled 265 northern pikeminnow stomachs from April through August 1997; 249 (94%) were from northern pikeminnow 200-349 mm in length. The abundance of prey items in diets of northern pikeminnow differed among sampling locations in 1996 (Figure 2). Crustaceans were the most abundant prey item by weight from northern pikeminnow stomachs collected in the tailrace (71.3%), Clearwater River Arm (84.9%), and Snake River Arm (90.6%). We found one juvenile salmonid in one northern pikeminnow collected from the tailrace-RZ. Juvenile salmonids were absent from stomachs of northern pikeminnow collected at the other locations in 1996.

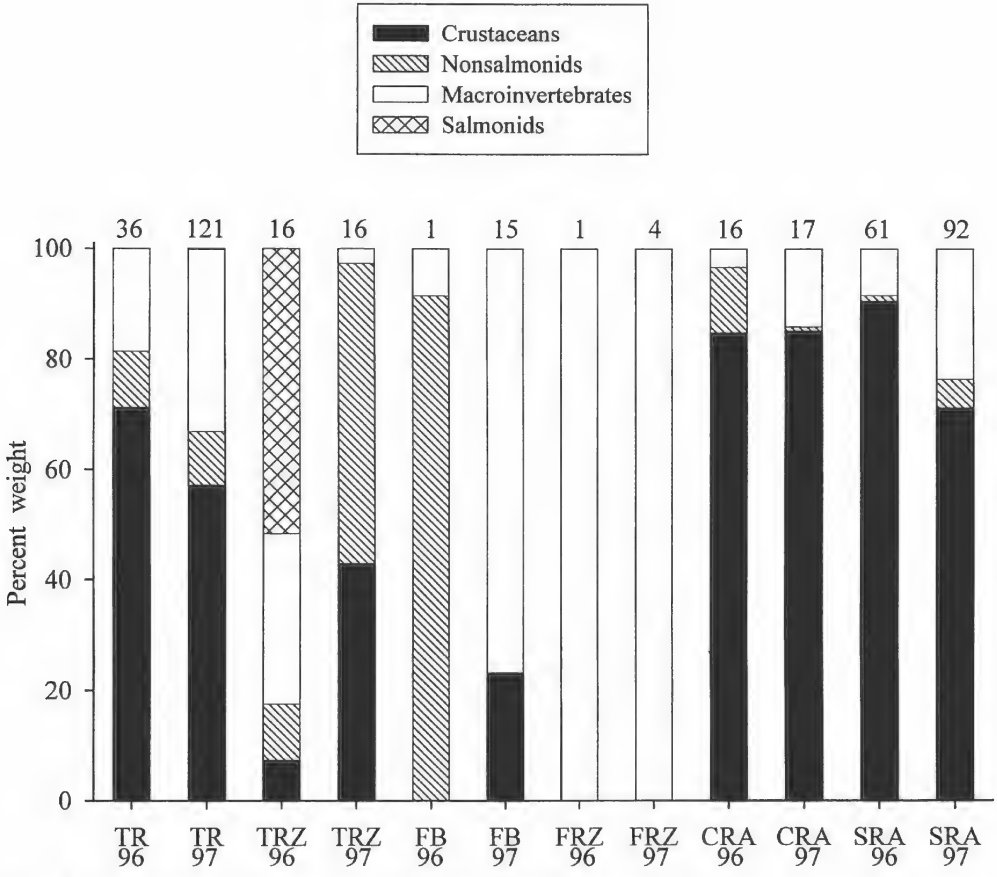


Figure 2. Spatial variation in diet composition by location of northern pikeminnow (n=396) collected in Lower Granite Reservoir and tailrace in 1996 and 1997. Locations are Lower Granite Dam tailrace (TR), tailrace restricted zone (TRZ), forebay (FB), forebay restricted zone (FRZ), Clearwater River arm (CRA), and Snake River arm (SRA). Numbers above bars indicate number of stomachs sampled at each location.

Diets of northern pikeminnow also differed among reservoir locations in 1997 (Figure 2). As in 1996, crustaceans were the dominant prey items by weight in northern pikeminnow stomachs collected from the tailrace (57.2%), Clearwater River Arm (85.2%), and the Snake River Arm (71.2%). Nonsalmonid fishes were the most abundant prey items by weight in the tailrace-RZ (54.3%), whereas macroinvertebrates accounted for 100% of the diet weight of four northern pikeminnow collected from the forebay-RZ. Juvenile salmonids accounted for 0.1% of the diet weight of 123 northern pikeminnow collected from the tailrace but were absent in stomach samples from all other locations.

## Discussion

Of the 648 northern pikeminnow captured 17% were large (>349 mm in length), the size range considered highly predatory on juvenile salmonids (Poe et al. 1991). We found the highest concentration of these large northern pikeminnow the tailrace-RZ, similar to findings at other Columbia (Beamesderfer and Rieman 1991) and Snake river dams (Ward et al. 1995).

Based on diet composition and their low abundance, we did not find that the northern pikeminnow was a major predator of juvenile salmonids in the tailrace and forebay of Lower Granite Dam in 1996 and 1997 (Figure 2). Our estimates of

predation of juvenile salmonids by northern pikeminnow are substantially less than those reported for the McNary Dam tailrace (Rieman et. al 1991). We suspected lower salmonid consumption than at the Lower Columbia River dams based on results from Ward et al. (1995) who reported the index of salmonid consumption decreased from downstream to upstream in the Columbia River basin. Although direct comparison is not possible, salmonid consumption in the Lower Granite tailrace was less in 1996 and 1997 than in 1991 (Ward et al. 1995). One apparent difference in habitat conditions between 1991 and 1996 and 1997 was that flows in the lower Snake River in the spring of 1996 and 1997 were considerably higher than those in 1991. In our study, the two salmonids found in northern pikeminnow stomach samples were collected from fish captured within 1 km of Lower Granite Dam. We hypothesize that the lower incidence of salmonids in northern pikeminnow stomachs was related to higher flows that resulted in northern pikeminnow displacement (Piaskowski 1998) or reduced sightability (Vinyard and O'Brien 1976).

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## Literature Cited

Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:439-447.

Bennett, D. H., P. M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential for improving warmwater fish habitat in the lower Snake River reservoirs. Completion Report, Number DACW68-79-C0057. U.S. Army Corps of Engineers, Walla Walla, Washington.

Bently, W. W., and H. L. Raymond. 1976. Delayed migrations of yearling chinook since completion of Lower Monumental and Little Goose Reservoirs on the Snake River. Transactions of the American Fisheries Society 105:422-424.

Chandler, J. A. 1993. Consumption rates and estimated total loss of juvenile salmonids by northern squawfish in Lower Granite Reservoir, Washington. M.S. Thesis, University of Idaho, Moscow, Idaho.

Connor, W. P., H. L. Burge, and D. H. Bennett. 1998. Detection of PIT-tagged subyearling chinook salmon at a Snake River Dam: Implications for summer flow augmentation. North American Journal of Fisheries Management 18:530-536.

Curet, T. 1993. Habitat use, food habits, and the influence of predation on subyearling chinook salmon in Lower Granite and Little Goose reservoirs. M.S. Thesis, University of Idaho, Moscow, Idaho.

Ebel, W. J., and H. L. Raymond. 1976. Effect of atmospheric gas saturation on salmon and steelhead trout of the Snake and Columbia rivers. U.S. National Marine Fisheries Service. Marine Fisheries Review 38:1-14.

Fish Passage Center. 1996. Fish Passage Center annual report, 1996. Fish Passage Center, Project 87-127, Bonneville Power Administration. Portland, Oregon.

Fish Passage Center. 1997. Fish Passage Center annual report, 1997. Fish Passage Center, Project 87-127, Bonneville Power Administration. Portland, Oregon.

Funk, W. H., C. M. Falter, and A. J. Lingg. 1985. Limnology of an impounded series in the lower Snake River. Unpublished Final Report. U.S. Army Corps of Engineers, Walla Walla, Washinton.

Hansel, H. C., S. D. Duke, P.T. Lofy, and G.A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of the American Fisheries Society 117:55-62.

Hofer, R. 1991. Digestion. Pages 413-425 *In* J. Winfield and J. S. Nelson (editors), Cyprinid Fishes: Systematics, Biology and Exploitation. Chapman and Hall, New York.

National Marine Fisheries Service. 1992. Endangered and threatened species; Threatened status for Snake River spring/summer chinook salmon, threatened status for the Snake River fall chinook salmon. Federal Register 57:78 (22 April 1992): 14,653-14,663.

Piaskowski, R. M. 1998. Distribution and movements of northern squawfish and smallmouth bass during operation of a surface bypass collection system for juvenile salmonids at Lower Granite Dam. M.S. Thesis, University of Idaho, Moscow, Idaho.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:405-420.

Raymond, H. L. 1968. Migration rates of yearling chinook salmon in the Columbia River. Transactions of the American Fisheries Society 97:356-359.

Rieman, B. E., and R. C. Beamesderfer. 1990. Dynamics of a northern squawfish population and the potential to reduce predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. North American Journal of Fisheries Management 10:228-241.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120: 448-458.

Rosentreter, N. 1977. Angling, biology, and genetics. American Fisheries Society, Bethesda, Maryland. Special Publication 10:79-83.

Scheaffer, R. L., W. Mendenhall, and L. Ott. 1990. Elementary Survey Sampling. 4th edition. Duxbury Press, North Scituate, Massachusetts.

Steinberger, L. W., and P. A. Larkin. 1974. Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus orgonensis*). Journal of the Fisheries Research. Board of Canada. 31:411-420.

Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:421-438.

Vinyard, G. L., and J.W. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal of the Fisheries Research Board of Canada 33:2845-2849.

Ward, D. L., J. H. Petersen, and J. J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. Transactions of the American Fisheries Society 124:321-334.

Weitkamp, D. E., and M. Katz. 1980. A review of dissolved gas supersaturation literature. Transactions of the American Fisheries Society 109:659-702.

Zaugg, W. S., E. F. Prentice, and F. W. Waknitz. 1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. Aquaculture 51:33-47.

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# Influence of Spring Runoff and Water Temperature on Hatch Date and Growth of Age-0 Largemouth Bass in a Montana Reservoir

## Abstract

Largemouth bass are a popular sport fish in Montana and the Northwest, however, maintaining quality angling is difficult. Montana is at the northern extent of the largemouth bass range and low water temperatures may limit recruitment by reducing the size fish attain entering the winter season. Little is known about how different flow and temperature regimes influence hatch date and growth of largemouth bass in a northern reservoir environment. Such information is important for predicting good year classes or planning population enhancement measures. Two years with disparate hydrographs and water temperature regimes were compared from a Montana reservoir. High flows and low water temperatures occurred in 1997 whereas the converse happened in 1998. Age-0 largemouth bass were sampled throughout the summer and fall of both years to estimate hatch date, growth rate, body condition, and length entering the winter season. The median hatch dates were in mid-July and 5 d earlier in 1998 than in 1997. Hatching began 12 d earlier in 1998. Spawning and hatching were controlled by spring runoff and were later than reported for lakes elsewhere in northwest Montana. Growth rate was higher in 1998 (0.76 mm/d) than 1997 (0.46 mm/d) from the date mean lengths were ~50 mm to early October. Higher growth rates and longer lengths were achieved by hatching early in a year with high water temperature. Length entering into winter was greater in 1998, averaging 87 mm versus 64 mm in 1997. Body condition was similar between years. Growth of age-0 fish appeared to cease by early October of both years. Growth rate had a greater effect on length of largemouth bass entering into winter than length of growing season.

## Introduction

Popularity of fishing for warm and coolwater fishes has increased in the Northwest (Bennett et al. 1991, McMahon and Bennett 1996). In northwest Montana, angling pressure on warm and coolwater species increased nearly 20% from 1991 to 1999 (McFarland and Hughes 1994, McFarland and Merideth 2000). The largemouth bass (*Micropterus salmoides)* is an introduced warmwater fish species that provides angling opportunity. Largemouth bass were introduced to the region sometime in the late 1880s (Lampman 1946). Since their introduction, however, habitats suitable for largemouth bass have increased with the building of 99 hydroelectric facilities throughout the Northwest (Bennett et al. 1991). In many cases, the increase in warmwater fish habitat corresponded to a decrease in coldwater habitats that supported highly valued trout and salmon fisheries. As a result, fishery managers have sought the enhancement of warmwater fish, such as largemouth bass, to provide recreational fishing that can be supported by existing habitat conditions. Yet, largemouth bass pose a difficult fishery to sustain from year-to-year in many Northwest waters (Bennett et al. 1991).

Variable year class strength is common in largemouth bass populations (Kramer and Smith 1962, Aggus and Elliot 1975, Bennett et al. 1991, Post et al. 1998). Much of the variability is the result of survival rates to age-1, making this period critical in determining recruitment to a fishery (Summerfelt 1975, Toneys and Coble 1979, Post et al. 1998). A possible reason for infrequent strong year classes is that the Northwest United States is the northern extent of the largemouth bass distribution. Overwinter mortality may regulate recruitment for species at the northern limits of their range (Shuter and Post 1990, Fullerton et al. 2000). Low water temperatures at northern latitudes slow growth rates and shorten the growing season by delaying hatch and extending winter (Post et al. 1998). Consequently, low water temperatures in northern waters result in small size of age-0 largemouth bass entering into winter. Larger size provides more energy reserves to avoid starvation (Gutreuter and Anderson 1985, Miranda and Hubbard 1994a) or predation (Miranda and Hubbard 1994b) during winter, thus increasing survival to age-1. Higher temperatures during the growing season have been related to stronger year classes for smallmouth bass (*M. dolomieu*) (Fry and Watt 1955) and other freshwater fishes (Craig and Kipling 1983).

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Longer largemouth bass become piscivorous sooner and maintain piscivory longer than smaller bass (Phillips et al. 1995), and greater piscivory has been related to greater growth (Aggus and Elliot 1975, Miller and Storck 1984). Other investigators have distinguished different growth rates between times of hatching (Miller and Storck 1984, Goodgame and Miranda 1993, Phillips et al. 1995). In these studies, early-hatched fish grew faster because of their greater ability to switch to a piscivorous diet. Coincident with this was the inability of age alone to account for much of the variation in length without considering time of hatch (e.g, early or late) largely because variation of length increased with increasing age. These studies found that increased variation in length with age was explained by time of hatch and that earlier hatched fish were longer at a particular age than later hatched fish. For example, at 50 d old a fish that hatched early tended to be longer than a fish hatched late.

Hatch date and growth rate interact to affect the length age-0 largemouth bass reach entering the winter season in several regions of the U.S., including a northern lake (Post et al. 1998), and midwestern (Miller and Storck 1984, Kohler et al. 1993) and southeastern reservoirs (Phillips et al. 1995). Information is lacking regarding the recruitment process in northwestern reservoirs. Such information could be useful in predicting year class strength and recruitment to a fishery and when assessing population enhancement measures (e.g., supplemental stocking or habitat enhancement). In this study, I obtained information on the recruitment process of largemouth bass in Noxon Rapids Reservoir, Montana by contrasting hatch date, growth, and length of fish entering into winter between two years with disparate flow and temperature regimes. I studied the population dynamics of age-0 largemouth bass with the following objectives: (1) evaluate the effect of water temperature, age, and hatch date on growth rate of age-0 largemouth bass within an annual cohort, (2) compare, between years, spring runoff (discharge) and water temperature and their influence on hatch date distribution, growth, and size entering winter, and (3) compare within-year population dynamics among-years.

## Study Area

Noxon Rapids Reservoir is located on the Clark Fork River ~225 km northwest of Missoula. The reservoir is ~732 m above sea level, encompasses nearly 3,200 ha, and was created to provide hydroelectric power. Typical operations are a weekly 1.2 m draw with a maximum 3.1 m draw during late winter or early spring. Trophic status ranges from oligotrophic at high flows during spring snowmelt to mesotrophic at low flows (Washington Water Power 1996). Maximum surface water temperatures typically are 20-25°C. Water retention is about 2 wk during summer low flows. The reservoir rarely stratifies, and then partially and for a short time. The reservoir inundated a deep river canyon to a level above much of the canyon walls. As a result, there are several bays and extensive flats that provide suitable habitat for largemouth bass. Flow capacity of the dam is ~1,550 $m^3/s$.

The fish community is dominated by Cyprinidae, including northern pikeminnow (*Ptychocheilus oregonensis*) and peamouth (*Mylocheilus caurinus*) (Washington Water Power 1995). Yellow perch (*Perca flavescens*) are abundant and stunted at ~200 mm. Largemouth bass and smallmouth bass are common. The few Salmonids are confined to coldwater refuges at tributary mouths and springs during summer. Species of Salmonidae include brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss)*, westslope cutthroat trout (*O. clarki lewisii*), bull trout (*Salvelinus confluentus*), lake trout (*S. namaycush*), lake whitefish (*Coregonus clupeaformis*), and mountain whitefish (*Prosopium williamsoni*).

## Methods

I used a 15.2 x 3.1 m bag seine with 10 mm mesh and a 1.2 x 1.2 m bag. Boat and backpack electrofishing were attempted to capture larger age-0 fish (Jackson and Noble 1995) but were ineffective due to growth of macrophytes in deep water. I sampled these deeper water habitats by deploying the seine into the macrophytes from a boat, then pulled it to shore. Sampling with only a bag seine may have underestimated the length of bass because seining tends to be biased toward smaller (<70 mm) fish (Jackson and Noble 1995).

Sampling was conducted throughout the summer and fall to capture the range of age-0 bass ages and lengths. This strategy insured sampling of similar aged fish during different times of the year and growing conditions. I sampled six times from 3 August to 11 October 1997, and five times from 3 August to 19 October 1998. No bass were

captured during the first two sampling occasions (3 and 11 August) in 1997. Sampling sites were intended to remain constant throughout the study, however, catch of largemouth bass varied spatially by season and year. Therefore, I sampled bass where desired sample sizes could be obtained while standardizing sites to the extent possible. Fish were collected from two to five sites on each sampling date. Length of fish (TL, mm) was recorded and specimens for otolith dissection and aging were taken to the laboratory. I sampled between 24 and 121 fish per sampling occasion.

### Water Temperature and Flow

Mean daily water temperature was recorded during summer (defined as 1 July-30 September) with thermographs taking readings 10 times a day. Thermographs were placed at two bays typical of young largemouth bass habitat. The operators of the dam provided data on river discharge. Mean daily summer water temperature was compared between years using a t-test ($P \leq 0.05$).

### Hatch Date

I counted daily rings on otoliths to estimate age and calculate hatch date following the methods of Taubert and Coble (1977) and Miller and Storck (1982). Because age-0 bass do not form a daily ring until they are about 5 d old, 5 d were added to the age determined by counting rings (Miller and Storck 1984). Hatch date was calculated by subtracting the age (d) from the sample date. Hatch date distributions were developed using otoliths from all samples in each year. Median and range of hatch dates were compared between years. Difference in median hatch dates was tested using a Mann-Whitney U-test ($P \leq 0.05$).

### Growth Rate

I compared growth rates between years by inspecting trajectory plots of mean length on sampling dates through summer and fall, and calculating mean daily growth rates (mm/d). Because growth rate is influenced by foraging capability (i.e., gape size that is length-dependent) (Lawrence 1958) and growing conditions (i.e., water temperature and forage availability), three aspects of daily growth rates were compared between years, (1) incremental and season-long (from first capture until maximum mean length), (2) from the dates when fish reached similar mean lengths until they reached the maximum mean length, and (3) across similar dates.

I investigated the influence of age, cumulative degrees (sum of mean daily water temperature from hatch to capture date), and hatch period (early or late) on growth rate of age-0 bass. Cumulative degrees described the combined effects of duration and intensity of temperature experienced. Hatch period was determined by dividing cohorts into early- and late-hatch fish. Early-hatch fish were hatched within the first one-third of the range of hatch dates and late-hatch fish were in the later two-thirds. This division allowed for sufficient separation of early-hatch fish whose contribution to recruitment may be significant, particularly in northern waters (e.g., Post et al. 1998), and avoided problems with small sample sizes. Pearson's product-moment correlation was used to test for significant relationships. Because cumulative degrees were a combined effect of age and temperature, I tested for differences in r between the age-length and cumulative degrees-length relationships for each year. Significant and greater r-values for the cumulative degrees-length relationship indicated greater variation explained ($r^2$, Zar 1999), and thus a significant influence of water temperature on growth rate. The effect of hatch period for each year was evaluated using analysis of covariance if slopes for age-length relationships were equal between hatch periods. Hatch period was the main effect with length the dependent variable and age the covariate. If slopes were unequal and significant, I visually inspected plots and compared slopes of regression lines to assess the rate of length gained with age. Non-linear data were transformed using ($x^3$) and ($\log_{10}$) to improve linearity. Statistical tests were considered significant at $P \leq 0.05$.

### Body Condition and Length Entering Winter

Condition was estimated using [transformed ($\log_{10}$)] length-weight correlations. To compare condition between years, I first tested for differences in the slopes of the length-weight relationship. If slopes were equal, I then tested for differences in the y-intercept to evaluate differences in weight at a given length. Length entering winter was estimated as the maximum mean length of age-0 largemouth bass during summer and fall sampling. A t-test was used to compare lengths

of bass entering winter between years. All tests were considered significant at $P \leq 0.05$.

## Results

### Water Temperature and Flow

Mean daily summer water temperature was significantly higher in 1998 than in 1997 ($P < 0.001$). In 1997, summer water temperature averaged 19.5°C whereas in 1998 water temperatures averaged 22.0°C. Higher summer water temperature was associated with lower discharge (Figure 1). In 1997, spring runoff from snowmelt resulted in high flows (peak flow of 3520 $m^3/s$) lasting from mid-May to late June. In 1998, spring snowmelt resulted in little flow (peak flow of 1636 $m^3/s$) and lasted from late May to early June. Suitable temperatures for spawning (15°C) were reached in early July 1997 and in early May 1998. In 1998, however, spring runoff decreased water temperature below 15°C from mid-May until early June. Rains created a second pulse in the hydrograph in mid- to late June that corresponded with stabilizing temperatures above 15°C. Water temperatures at the end of the growing season dropped precipitously and became similar between years. From 1 October-18 October, water temperatures dropped from 16.9° to 13°C in 1997 and from 18.6° to 13.5°C in 1998.

### Hatch Date and Periods

The median hatch dates were significantly different between years ($P < 0.05$; Figure 1). Median hatch date was five days earlier in 1998 (13 July) than in 1997 (18 July). Hatching began 12 d earlier in 1998 than in 1997 but ended on the same date in both years. Hatch dates ranged from 3 July to 17 August in 1997 (46 d long) and 21 June to 17 August (58 d long) in 1998. Hatching started when temperatures reached about 15°C, and peak hatch occurred in the second week of July in both years. In 1998, hatching slowed from early to mid-July in response to stabilized water temperatures from mid- to late June. As a result, there was an earlier hatch mode in early July and later hatch mode in mid-July.

Hatch periods differed between years, corresponding to the different hatch date distributions. The early-hatch period was 3-17 July (15 d) in 1997, and 21 June-9 July (19 d) in 1998 (Figure 1). Early-hatch fish in 1998 were generally hatched before early-hatch fish in 1997. The two-mode distribution in 1998 resulted in proportionally less of the hatch occurring in the early period than in 1997 when the distribution was skewed towards earlier dates. In 1998, 31% (n = 67) of the hatch occurred in the early period, and in 1997, 49% (n = 143) of the hatch was in the early period.

### Growth Rate, Body Condition, and Length Entering Winter

Growth rate was greater in 1998 than in 1997 (Figure 2). Mean lengths of age-0 largemouth bass ranged from 48 mm (SE = 0.66) to 64 mm (SE = 1.3) in 1997 and from 39 mm (SE = 1.4) to 87 mm (SE = 1.6) in 1998. Precision of mean length estimates was high (mean SE = 1.5 mm), so estimates of growth rates should be similarly precise. In both years, growth rate was negative and the lowest from early to mid-October. Maximum mean lengths were recorded in early October, suggesting the end of the growing season was between early and mid-October in each year. The first date of capture was 29 August in 1997 and 5 August in 1998. Mean bass lengths were most similar on 29 August 1997 and 13 August 1998. Mean growth rates from first capture to maximum mean length was 0.46 mm/d in 1997 and 0.83 mm/d in 1998. Growth rate was highest in 1997 from 19 September to 3 October when fish grew from a mean of 53 to 64 mm (0.69 mm/d). In 1998, the highest growth rate (1.15 mm/d) was recorded from 13 August to 1 September when fish grew from a mean of 49 to 70 mm. From dates when bass were similar in mean length (29 August 1997 and 13 August 1998) to maximum mean lengths in early October, growth rate was higher in 1998 (0.76 mm/d) than in 1997 (0.46 mm/d). This suggests that fish in 1998 grew faster despite having similar initial foraging capabilities as those in 1997. Similar dates of capture were the periods of 29 August to 3 October 1997 and 1 September to 1 October 1998. During this time, growth rate was higher in 1998 (0.57 mm/d) versus 1997 (0.46 mm/d) again suggesting better growing conditions in 1998. Growth trajectories differed. In 1997, the trajectory (growth rate) increased with time whereas in 1998 it decreased. The mean length estimates for fish on 1 September and 1 October 1998 are likely conservative because of the bias seine sampling has for fish <70mm, particularly for the October sample when fish were larger.

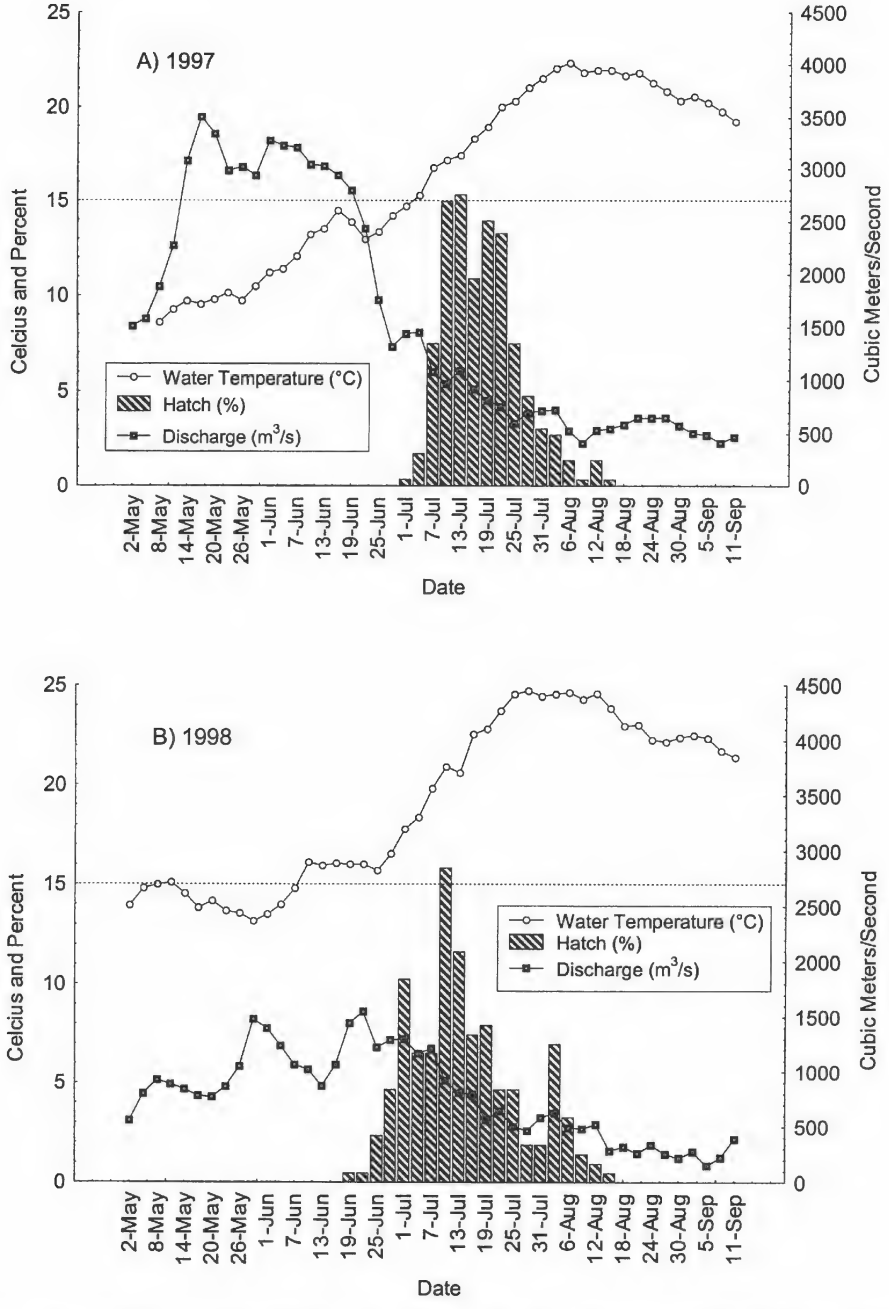


Figure 1. Relationship between flow, water temperature, and largemouth bass hatch date in Noxon Rapids Reservoir, Montana during A) 1997 (n = 294) and B) 1998 (n = 215). Dashed line at 15°C was added to illustrate when water temperature reached suitable temperatures for spawning. Hatch dates are grouped into 3 d periods.

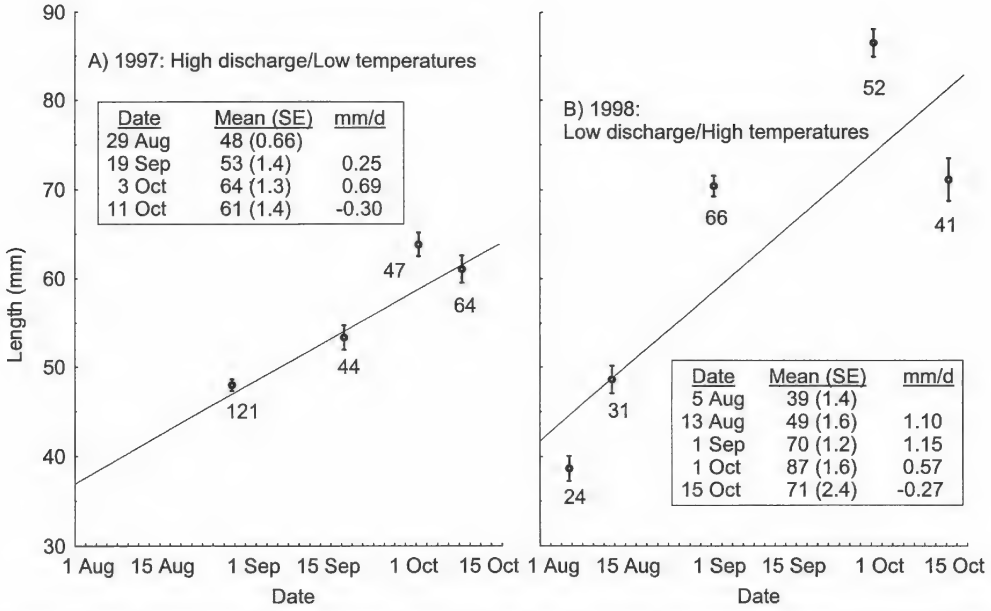


Figure 2. Growth trajectories for age-0 largemouth bass in Noxon Rapids Reservoir during summer through fall of A) 1997 and B) 1998. Regression line added for visual comparison of growth rate (slope) across sampling dates. Shown at each date is the sample size and mean ± standard error.

Length entering into the winter season was significantly greater in 1998 than in 1997, whereas condition was similar. Largemouth bass entered into winter at a mean length of 64 mm (SE = 1.3) in 1997 and a mean length of 87 mm in 1998 (SE = 1.2), so fish averaged 23 mm larger in 1998 than in 1997 ($P < 0.001$, Figure 2). These mean lengths were recorded on 1 October in 1997 and 3 October in 1998. Condition of age-0 fish was similar between the two years. Correlations of length and weight [both transformed using ($\log_{10}$)] were significant (r = 0.99, $P < 0.001$) for both years. Slopes and intercepts were not significantly different (slope = 2.94 and intercept = -4.75 in 1997, and slope = 2.97 and intercept = -4.80 in 1998).

Age-length correlations were significant ($P < 0.001$) for both years suggesting that older fish were longer (Figure 3). Age explained 55% of the variation (r = 0.74) in length in 1997 and 71% (r = 0.84) in 1998 using $\log_{10}$ transformations of age and length. For the 1997 data, transformations of age ($x^3$ and $\log_{10}$) and length ($\log_{10}$) did not result in increased r-values ($r \leq 0.74$), so they were not used. The relationship between cumulative temperature and length resulted in significant correlations ($P < 0.001$) in both years and higher r-values (r = 0.75 in 1997 and 0.87 in 1998) than age-length relationships, but did not describe a significantly greater proportion of variance in either year. Mean temperatures experienced by individual bass ranged from 19.1 to 22.5°C in 1997 and 20.5 to 25.2°C in 1998.

Early hatching resulted in greater length in 1997 and 1998 (Figure 3). For 1997, hatch periods had significant correlations (r = 0.74 for early-hatch and 0.76 for late-hatch, $P < 0.001$ for both) and similar slopes (slopes = 0.53 for early-hatch and 0.60 for late-hatch). Adjusted means of length were significantly different using analysis of covariance ($P < 0.05$). Adjusted mean was 55.4 mm for early-hatch fish and 53.1 mm for late-hatch fish, indicating a 2.3 mm advantage for early-hatch fish at a given age. In 1998, correlations using $\log_{10}$ transformations of age and length were significant for both hatch periods (r = 0.92 for early-hatch, r = 0.83 for late-hatch, and $P < 0.001$ for both periods), but slopes were not equal ($P < 0.001$).

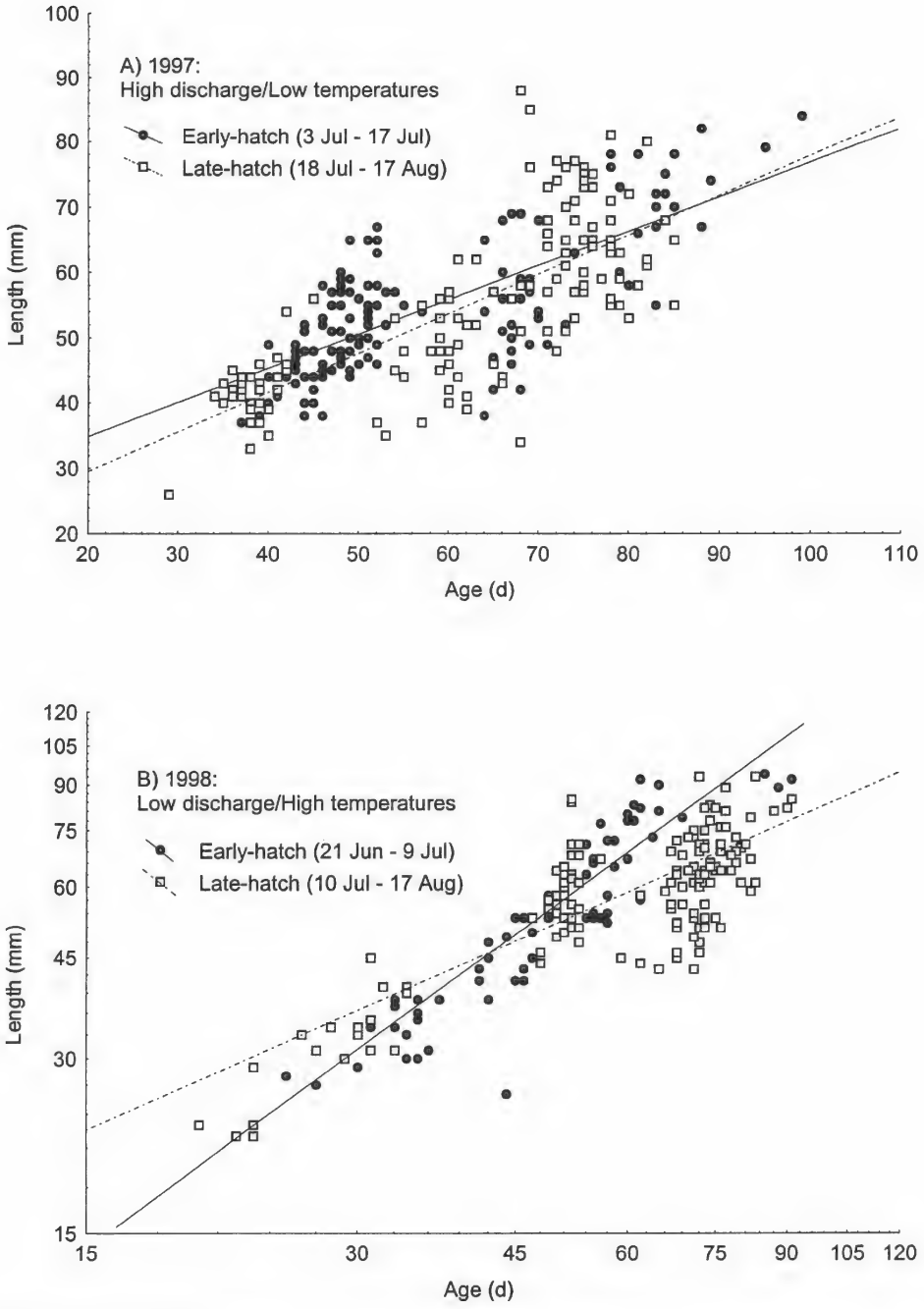


Figure 3. Relationships between age and length by hatch period for age-0 largemouth bass in Noxon Rapids Reservoir during the summers of A) 1997 and B) 1998. Note difference in scales.

The slope for early-hatch fish was 1.18 versus 0.71 for late-hatch fish. The greater slope suggests that length was gained more rapidly with increasing age in 1998. Inspection of the scatterplot for 1998 (Figure 3B) indicated that early-hatch fish were slightly smaller than late-hatch fish from about 30 to 45 d then were larger at older ages. According to correlations, a 30 d old early-hatch fish averaged 30 mm versus 35 mm for late-hatch fish. At 75 d old, early-hatch fish were 88 mm and late-hatch fish 68 mm. The division of the overall age-length relationship in 1998 (n = 215) into hatch periods helped explain part of the variation in length at ages over 45 d old. This was indicated by the generally higher r-values for early- and late-hatch fish (r = 0.92 and 0.83, respectively) versus the overall age-length relationship (r = 0.84). The lower r-value for late-hatch versus early-hatch fish was largely due to remaining and higher variation of length at ages over 45 d.

## Discussion

Largemouth bass in Noxon Rapids Reservoir hatched earlier in 1998 (median difference = 5 d, start 12 d earlier) when flows were lower and temperatures warmed more quickly. Spawning and hatching were largely controlled by snowmelt and spring runoff and, as a result, were later than reported for lakes in the same region of Montana. Within a year, earlier hatching resulted in faster growth, presumably because of increased piscivory. Only 1998 had a large enough difference in growth rate between early- and late-hatch to be of biological significance, however. Water temperatures experienced by individual fish did not result in different growth rates within an annual cohort. Highest growth rates were achieved by hatching early in the year with higher water temperatures (i.e., 1998). Among years, differences in length of age-0 largemouth bass entering winter between 1997 and 1998 was primarily due to differences in growth rate, whereas growing season was less important because of its low variability. Water temperature was probably the most influential factor for differences in growth rate between years. Body condition was similar between years. Age-0 largemouth bass in Noxon Rapids Reservoir achieved greater lengths entering winter more by growing faster than by having longer to grow.

Spring runoff affected the timing and duration of hatching for largemouth bass in Noxon Rapids Reservoir (Figure 1). Spring runoff mediates the effects of warming air temperatures in May and June by increasing the volume of cold water coming from snowmelt. Later hatching dates were likely the result of later spawning due to low water temperature. Water temperature in concert with photoperiod controls the onset of spawning. Bass spawn between 15 and 24°C (Kramer and Smith 1962). In northwest Montana lakes, largemouth bass spawning begins in mid-May to late June depending on water temperatures (Walker-Smith 1995), indicating that photoperiod would be suitable in May at Noxon Rapids Reservoir. However, at Noxon Rapids Reservoir, hatching began in late June in 1998 and early July in 1997 after high flow and when water temperatures were above 15°C and suitable for spawning. In 1998, spring rains slowed hatching in early July, even though water temperature exceeded 15°C. The lack of a rising trend in temperature appeared to reduce hatching and probably spawning. A similar response to temperature was reported in an Illinois reservoir where rising water temperatures above 15°C stimulated largemouth bass to spawn (Miller and Storck 1984).

My results suggested that growth of age-0 fish ceased when temperatures were still suitable for growth (Figure 2). The growing season ends when water temperatures fall below 10°C (Coutant 1975, Adams et al. 1982). However, water temperatures in Noxon Rapids Reservoir were at ~13°C in mid-October of both years, suggesting conditions were still favorable for growth. Immediately prior to the decrease in length of fish according to mid-October sampling was a cold front. Maximum air temperatures dropped from 28 to <15°C on 2-4 October 1997 and 3-5 October 1998 (U.S. Forest Service weather station near Noxon Rapids Reservoir, unpublished data, 1999). Movement by age-0 largemouth bass out of littoral areas to deeper water in response to cold fronts was observed in two Montana lakes (Walker-Smith 1995) and reported elsewhere (Coutant 1975). In Noxon Rapids Reservoir, smaller age-0 largemouth bass may use shallow water to avoid predators despite the potential for starvation because of low, fluctuating temperatures (Miranda and Hubbard 1994a, Garvey et al. 1998). Thus, the fish sampled on

the last sampling date in both years consisted of the smaller age-0 bass within their respective year classes, whereas larger individuals moved to deeper water and were not sampled.

Earlier hatching resulted in longer bass in both 1997 and 1998, but was more important in 1998. Being hatched earlier simply allowed fish more time to grow (get older) and reach longer lengths (Figures 2 and 3). In addition to having a longer growing season, early-hatch fish grew faster than late-hatch fish in both years. The benefit of early hatching in 1997 was small (an additional 2.3 mm in length), suggesting that this difference was not biologically important. However, in 1998, earlier hatching had a greater benefit (20 mm for a 75 d old fish). Conversely, bass that experienced higher water temperatures than fish of similar age were not longer. This suggests that, within an annual cohort, early-hatch fish grew faster and longer than late-hatch fish because of foraging opportunity rather than higher water temperatures. Information on diet was not collected in this study but past studies support this hypothesis. Growth rate of age-0 largemouth bass increases with the rate of piscivory (Aggus and Elliot 1975, Miller and Storck 1984) and is higher for earlier hatched fish (Maceina and Isely 1986, Goodgame and Miranda 1993). Furthermore, Phillips et al. (1995) linked hatch date and piscivory directly to growth rate of age-0 largemouth bass by finding that early-hatch fish were more piscivorous and grew faster than later-hatch fish in a North Carolina reservoir.

Water temperature among years is the most probable and influential reason for observed differences in largemouth bass annual growth rates and length entering winter. Mean daily summer water temperatures in 1997 (19.5°C) and 1998 (22.0°C) were below the optimum for growth (Figure 1). Optimal temperature for growth of largemouth bass is 27.5°C (Coutant 1975). Growth rate increases to the optimum. Therefore, higher temperatures, as long as they are below the optimum, should correspond to higher growth rates. This suggests that growth rates would be higher in 1998 than in 1997, as was seen in this study.

Growth rate had a greater influence on length of largemouth bass entering the winter season in Noxon Rapids Reservoir than length of growing season during this study. Using growth rates when foraging capabilities were initially equal, the increased growth rate estimated in 1998 (0.76 mm/d) versus 1997 (0.46 mm/d) added an additional 26 mm for a fish 85 d old fish. Generally, the growing season was from ~15 July to 10 Oct or 85 d in Noxon Rapids Reservoir. Furthermore, the difference of 26 mm corresponds well with the difference in estimates from sampling (23 mm) (Figure 2). Conversely, length of growing season was relatively similar between 1997 and 1998. The beginning of the growing season was 5-12 d earlier in 1998 (as indicated by the difference of median and range of hatch dates) (Figure 1) and both seasons ended at similar times according to growth trajectories and water temperature. Again, using the predicted growth rates, and a 5 to 12 d extension in the growing season, the additional time from earlier hatching in 1998 adds only 2 to 9 mm in length.

Further study is needed on the relationship of growth to number of fish, mortality rates through summer and winter, and recruitment to the population. Investigation of the relationship between length entering winter and survival to age-1 and the fishery is needed. Overwinter survival is size-dependent in some systems (Adams et al. 1982; Bowles 1985; Post et al. 1998; Miranda and Hubbard 1994a, 1994b) but not others (Hatch 1991, Kohler et al. 1993, Jackson and Noble 2000). Garvey et al. (1998) reported variable size-dependent survival across a range of northern and southern waters. Results of this study identify key environmental conditions and population factors that influence hatch timing and growth, two critical elements of the recruitment process.

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## Literature Cited


Adams, S. M., R. B. Mclean, and M. M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Canadian Journal of Fisheries and Aquatic Sciences 39:1175-1184.

Aggus, L. R., and G. V. Elliott. 1975. Effects of cover and food on year class strength of largemouth bass. Pages 317-322 *In* H. Clepper (editor), Black Bass Biology and Management. Sport Fishing Institute, Washington, D. C.

Bennett, D. H., D. R. Hatch, and M. D. Liter. 1991. Managing largemouth bass in the Northwest: A game of recruitment, protection, and patience. Pages 313-322 *In* J. L. Cooper and R. H. Hamre (editors), Warmwater Fisheries Symposium I, USDA Forest Service General Technical Report RM-207, Fort Collins, Colorado.

Bowles, E. C. 1985. Recruitment and survival of young-of-the-year largemouth bass Micropterus salmoides in the Couer d'Alene Lake system, Idaho. M. S. thesis. University of Idaho, Moscow, Idaho.

Coutant, C. C. 1975. Responses of bass to natural and artificial temperature regimes. Pages 272-285 *In* H. Clepper (editor), Black Bass Biology and Management. Sport Fishing Institute, Washington, D. C.

Craig, J. F., and C. Kipling. 1983. Reproduction effort versus the environment; case histories of Windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. Journal of Fish Biology 22:713-727.

Fry, F. E. J., and K. E. F. Watt. 1955. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Transactions of the American Fisheries Society 85:135-143.

Fullerton, A. H., J. E. Garvey, R. A. Wright, and R. A. Stein. 2000. Overwinter growth and survival of largemouth bass: Interactions among, size, food, origin, and winter severity. Transactions of the American Fisheries Society 129:1-12.

Garvey, J. E., R. A. Wright, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. Canadian Journal of Fisheries and Aquatic Sciences 55:2414-2424.

Goodgame, L. S., and L. E. Miranda. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. Transactions of the American Fisheries Society 122:131-138.

Gutreuter, S. J., and R. O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass populations. Transactions of the American Fisheries Society 114:317-327.

Hatch, D. R. 1991. Factors limiting largemouth bass in Long Lake, Spokane County, Washington. M.S. thesis, University of Idaho, Moscow, Idaho.

Jackson, J. R., and R. L. Noble. 1995. Selectivity of sampling methods for juvenile largemouth bass in assessments of recruitment processes. North American Journal of Fisheries Management 15:408-418.

Jackson, J. R., and R. L. Noble. 2000. First-year cohort dynamics and overwinter mortality of juvenile largemouth bass. Transactions of the American Fisheries Society 129:716-726.

Kramer, R. H., and L. L. Smith, Jr. 1962. Formation of year classes in largemouth bass. Transactions of the American Fisheries Society 91:29-41.

Kohler, C. C., R. J. Sheehan, and J. J. Sweatman. 1993. Largemouth bass hatching success and first-winter survival in two Illinois reservoirs. North American Journal of Fisheries Management 13:125-133.

Lampman, B. H. 1946. The Coming of the Pond Fishes. Metropolitan Press, Portland, Oregon.

Lawrence, J. M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 11(1957): 220-225.

Maceina, M. J., and J. J. Isely. 1986. Factors affecting growth of an initial largemouth bass year class in a new Texas reservoir. Journal of Freshwater Ecology 3:485-492.

McFarland, R. C., and J. E. Hughes. 1994. Montana statewide angling pressure mail survey 1991. Unpublished report on file at Montana Department of Fish, Wildlife and Parks, Helena, Montana.

McFarland, R. C., and D. Meredith. 2000. Montana statewide angling pressure mail survey 1999. Unpublished report on file at Montana Department of Fish, Wildlife and Parks, Helena, Montana.

McMahon, T. E., and D. H. Bennett. 1996. Walleye and northern pike: boost or bane to Northwest fisheries? Fisheries 21:6-13.

Miller, S. J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Transactions of the American Fisheries Society 111:527-530.

Miller, S. J., and T. Storck. 1984. Temporal spawning distribution of largemouth bass and young-of-the-year growth, determined from daily otolith rings. Transactions of the American Fisheries Society 113:571-578.

Miranda, L. E., and W. D. Hubbard. 1994a. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80-87.

Miranda, L. E., and W. D. Hubbard. 1994b. Winter survival of age-0 largemouth bass relative to size, predation, and shelter. North American Journal of Fisheries Management 14:773-780.

Phillips, J. M., J. R. Jackson, and R. L. Noble. 1995. Hatching date influence on age-specific diet and growth of age-0 largemouth bass. Transactions of the American Fisheries Society 124:370-379.

Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Canadian Journal of Fisheries and Aquatic Sciences 55:2588-2600.

Shuter, B. J., and Post, J. R. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Summerfelt, R. C. 1975. Relationship between weather and year class strength of largemouth bass. Pages 166-174 *In* H. Clepper, editor, Black Bass Biology and Management. Sport Fishing Institute, Washington, D.C.

Taubert, B. C., and D. W. Coble. 1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. Journal of the Fisheries Research Board of Canada 34:332-340.

Toneys, M. L., and D. W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. Transactions of the American Fisheries Society 108:415-419.

United States Forest Service. 1999. Unpublished data on air temperature on file at Cabinet Ranger District, Kootenai National Forest, Trout Creek, Montana.

Walker-Smith, K. P. 1995. Environmental and biological factors limiting reproduction, recruitment and growth of largemouth bass in Seeley and Echo Lakes, Montana. M.S. thesis, University of Montana, Missoula, Montana.

Washington Water Power. 1995. Fish community assessment on Cabinet Gorge and Noxon Rapids Reservoirs. Unpublished report on file at Avista Corporation, Spokane, Washington.

Washington Water Power. 1996. Water quality and limnological evaluations on the lower Clark Fork River-a supplemental report. Unpublished report on file at Avista Corporation, Spokane, Washington.

Zar, J. H. 1999. Biostatistical Analysis, third edition. Prentice-Hall, Englewood Cliffs, New Jersey.

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# Use of Similar Habitat by Cutthroat Trout and Brown Trout in a Regulated River During Winter

## Abstract

Few differences in habitat use were observed between cutthroat trout and brown trout during winter in the Shoshone River, a regulated river in northwestern Wyoming. Radio-tagged fish of 20-30 cm total length were found in pool habitat five to six times more frequently than would be expected if they were using pools in proportion to pool availability. Nevertheless, run habitat was most frequently used by both species. The microhabitat characteristics at locations of each species were similar when in both pools and runs, however, habitat use was variable suggesting that a variety of microhabitats were suitable over-wintering habitat. Brown trout were more frequently associated with boulder cover than were cutthroat trout. Cutthroat trout used large pools that provided refuge from high water velocities more frequently that brown trout. Cutthroat trout and brown trout were found at similar distances from the bank except in late February when cutthroat trout were farther from the bank. Both species moved frequently during the winter, but cutthroat trout showed a greater propensity than brown trout to move long distances. This study suggests that during a mild winter in a stable environment, these species were able to overwinter successfully in a variety of habitats.

## Introduction

In regulated rivers of western North America, discharge from upstream impoundments is often reduced to annual lows during fall and winter after the irrigation season. The habitat constriction associated with decreased discharge may reduce habitat segregation among multiple populations of introduced salmonids. Rainbow trout (*Oncorhynchus mykiss*) or cutthroat trout (*O. clarki*) are often reared in hatcheries and stocked into regulated rivers (Wiley et al. 1993) where brown trout (*Salmo trutta*) have been introduced and have become naturalized (Heidinger 1993). While studies have been conducted on habitat preferences and competition among native and introduced salmonids, little comparative research has been conducted in regulated rivers among combinations of non-natives, especially during winter when habitat limitation may be most severe. The purpose of our study was to examine one combination of non-natives, sympatric populations of cutthroat trout and brown trout, in a regulated river during winter.

The physiological constraints placed on fish at low water temperatures are reflected in their habitat use and movement during winter. Pools are important areas for stream-dwelling salmonids during winter that provide decreased water velocities and protection from harsh environmental conditions and predation (Swales et al. 1986, Heggenes et al. 1993, Brown and Mackay 1995, Jakober et al. 1998, Simpkins et al. 2000a). Use of cover by salmonids appears to increase in the winter. Several studies have reported that salmonids suspend diurnal activity and conceal themselves when temperatures drop below 8-10°C (Rimmer et al. 1983, Griffith and Smith 1993, Fraser et al. 1995, Valdimarsson et al. 1997). However, salmonids may not cease activity entirely as they have been observed feeding during the day when water temperatures were substantially less than 8°C (Needham and Jones 1959, Pirhonen et al. 1997, Simpkins et al. 2000b).

Most studies of salmonid movement in winter have shown that mobility is decreased when compared to other times of year (Hilderbrand and Kershner 2000) and is most often related to changes in environmental conditions (Brown and Mackay 1995, Simpkins et al. 2000a). However, the bulk of previous research was conducted in natural-flowing streams that maybe subject to greater environmental variability and potentially harsh environmental conditions, such as river ice formation.

Despite similar body forms, there are contrasts in habitat use between cutthroat trout and other

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salmonids when in sympatry. When cutthroat trout and bull trout (*Salvelinus confluentus*) were studied in Montana (Nakano et al. 1992) and cutthroat trout and brook trout (*Salvelinus fontinalis*) were assessed in Idaho (Griffith 1972), cutthroat trout were more frequently found at locations farther from structures than either bull trout or brook trout.

While there have not been any direct comparisons of cutthroat trout and brown trout in a natural setting, studies of habitat use by brown trout suggest there may be differences between the species. Brown trout are a highly cover-oriented species often occupying positions downstream from structures that create feeding stations, areas with slow water in close proximity to fast water (Chapman and Bjornn 1969, Fausch and White 1981, Bachman 1984, Greenberg et al. 1996, Haugen and Rygg 1996, Quinn and Kwak 2000). This contrasts with the open-water, swift-flowing environment often used by cutthroat trout.

We wanted to know if there would be detectable differences in habitat use by cutthroat trout and brown trout that are placed in unnatural sympatry in a regulated river during winter. Our objective was to assess the similarity and differences in winter habitat use between cutthroat trout and brown trout in a regulated river where these two introduced species dominate the salmonid community. No research has been conducted during winter when lower water temperatures and habitat limitations could result in substantial overlap in habitat use between the species (Chapman 1966). Because of the environmental stability and higher water temperatures associated with river regulation, we expected to observe habitat-use patterns and spatial segregation similar to previous research.

## Study Area

This research was conducted in the Shoshone River, a regulated river in northwestern Wyoming. Discharge is controlled by Buffalo Bill Dam, located ~11 km west of Cody, Wyoming (Figure 1). Discharge during winter 1997-1998 was relatively stable at 13.8-14.8 $m^3/s$.

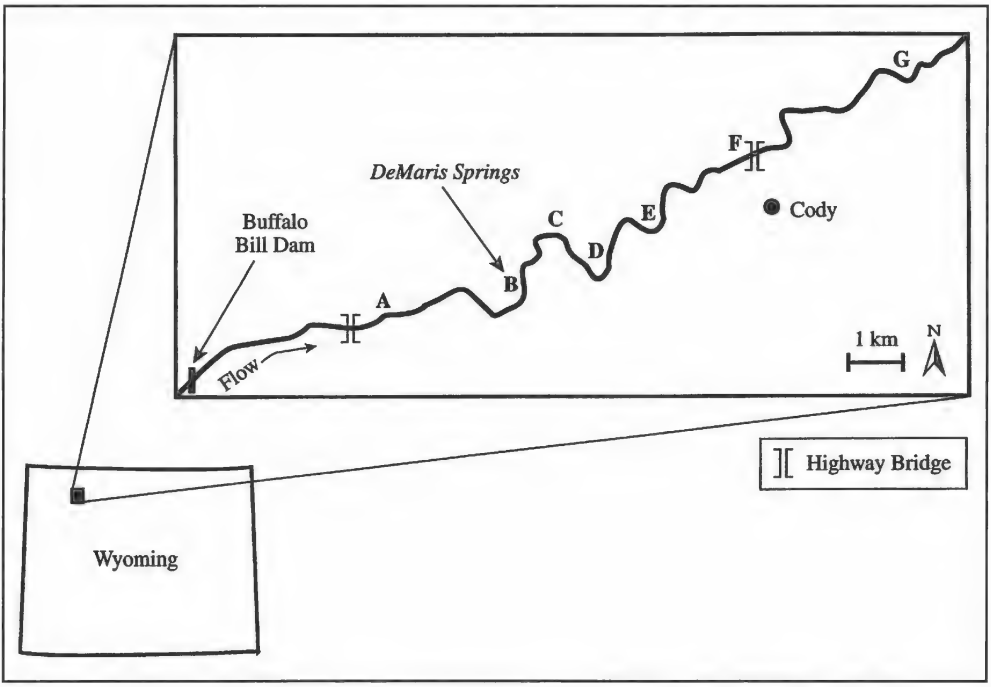


Figure 1. The study reach and water temperature sampling sites in the Shoshone River. Letters indicate water quality monitoring sites. Habitat availability and use were monitored between sites E and G.

The fine-spotted form of Yellowstone cutthroat trout (*O. clarki bouvieri)* that is native to the Snake River watershed is stocked annually downstream from Buffalo Bill Dam during the early summer. By October cutthroat trout reach 20-30 cm total length (TL). Brown trout were introduced in the 1930s and have been self-sustaining downstream from Buffalo Bill Dam since the 1960s. The density of each species has been estimated to be about 500 fish/km (Steven Yekel, Wyoming Game and Fish Department, personal communication).

## Methods

Seven recording thermographs were placed at approximate 2-km intervals downstream from Buffalo Bill Dam from DeMaris Springs to the downstream end of the study reach (Figure 1). The most downstream sampling site was 27 km downstream from Buffalo Bill Dam. Thermographs were set to record at 30-min intervals from 15 November 1997 through 31 March 1998.

The 5-km study reach was divided into 50 segments each 100-m in length and a transect was randomly placed at 0, 25, 50, or 75 m down from the upstream end of each segment. Habitat availability was measured within a series of 4-m-diameter circles evenly spaced along each transect. Spacing of sampling areas was determined by dividing the transect wetted width by the number of sampling areas that could be placed along the transect. For example, a transect with a wetted width of 36 m would have nine sampling areas with 4 m between adjacent centerpoints. Both microhabitat and mesohabitat features were described and assessed. Microhabitat features were specific to the 4-m-diameter sampling in which the fish occurred. Mesohabitat features were measures of larger-scale habitat features within the study reach.

Microhabitat features measured within each sampling area included minimum and maximum water depth, minimum and maximum water velocity, substrate composition, and presence of cover. Substrate composition was estimated by determining the area of each of six substrate size classes present within each sampling area. Size classes ranged from silt/sand (size 1) to bedrock (size 6) and the area of each size class was estimated to the nearest 10%. We used a weighted average to calculate the mean substrate size within each sampling area. Cover was classified based on the physical features associated with its formation—boulders, aquatic vegetation, or deep-water cover. Deep-water cover was identified as any area where the water velocities were near zero that lacked an associated structural feature, such as a boulder (Wesche et al. 1987). To be considered cover, any area or structural feature had to have a maximum water depth of at least 0.4 m to provide an overhead cover component. Vertical relief and water velocity gradients were estimated by subtracting a minimum depth or velocity value from the corresponding maximum. A detailed description of our habitat sampling methodology can be found in Dare and Hubert (2000).

Each sampling area was classified as one of three mesohabitat types: pool, run, or riffle in a manner similar to Rimmer et al. (1983) with the quantitative characteristics of each mesohabitat type modified to characterize the Shoshone River more accurately. Pools were areas having 1.50-m maximum depth, or >0.75-m maximum depth and <0.30-m/s maximum water velocity. Runs were intermediate areas having 0.30-1.50 m maximum depth, intermediate water velocities, and no surface turbulence. Riffles were stream areas having <0.30-m maximum depth, or <0.75-m maximum depth and >0.65-m/s minimum water velocity.

Twenty cutthroat trout and 20 brown trout (23-30 cm TL) were collected by angling and electrofishing on 13-17 November 1997. A radio transmitter (Advanced Telemetry Systems Model 357; 48.200-48.980 Mhz, mean weight 3.0 g; whip antenna length: 10 cm) was surgically implanted into the abdomen following the technique of Bidgood (1980). After a period of recovery (30-120 min) each fish was released near its point of capture.

Fish were located every 2-4 d using a receiver and handheld loop antenna from 22 November 1997 through 28 February 1998. Fish were tracked from a boat or from the bank, and fish locations were determined using two-point triangulation (Simpkins and Hubert 1998). Upon locating a fish we described microhabitat and mesohabitat features at the location within a few minutes of finding the fish. Microhabitat and mesohabitat features were measured or described within an area having a 2-m radius to collect data that were consistent with the habitat availability measurements. Microhabitat at an individual location was the

depth, velocity, substrate, and cover present with the 2-m diameter sampling area. Based on the depth and velocity characteristics we characterized each location as one of the three mesohabitats. Sampling methodologies for habitat availability and habitat use data were identical. The distance of a fish position from the bank was determined by measuring the straight-line distance (m) from the triangulated fish location to the nearest stream bank. Fish movement distance (straight-line distance within the stream channel) between consecutive locations was measured (m) with a tape if less than 100 m, or estimated from 1:24,000 scale topographic maps if greater than 100 m. The resolution of the maps was sufficient to identify the fish location to within 5 m, therefore only movements greater than 5 m were recorded.

We assessed the effect of fish length (within each species) on microhabitat use and movement using simple-linear regression. No significant relationships were found between fish length and water depth and water velocity use or movement, so we discounted fish length as a source of variability in microhabitat use and movement patterns. Additionally, neither species was observed in riffle habitat, therefore, this habitat type was excluded from the analysis of mesohabitat use.

We made separate comparisons of microhabitat use by cutthroat trout and brown trout in pools and runs using individual fish as the sampling unit. Fish were included in an analysis if they were observed at least five times within a mesohabitat type. To discern differences in mesohabitat use, we calculated the proportion of observations of individual fish of each species recorded in pools and runs and compared the proportions using a two-sample t-test. For each test a one-sided alternative hypothesis was used. We analyzed microhabitat use within each mesohabitat type to remove variation associated with the differences in the physical characteristics of pools and runs. For each individual we calculated a mean for each continuous microhabitat variable and then used a two-sample t-test to compare the suite of cutthroat trout individual means to the suite of brown trout individual means. To test for differences in cover types used by cutthroat trout and brown trout within each mesohabitat type, we also used a two-sample t-test. We calculated the proportion of locations of each individual having boulder cover or deep-water cover present. Given the expected differences between the two species, we used a one-sided alternative hypothesis that cutthroat trout used boulder cover less frequently and deep-water cover more frequently than brown trout.

The mean distance from the bank at locations of each species was calculated using data from dates when we observed at least 10 individuals of each species. We used time-series plots to determine if there was a trend through the winter in mean distance from the bank for each species.

To test if the frequency of movements differed between cutthroat trout and brown trout, we calculated the proportion of observations of individuals of each species made at new versus previously held locations. Proportions for each species were compared using a two-sample t-test. We compared movement distances by calculating the mean movement distance during each month of the study for individuals of each species and assessing differences using a two-sample t-test for each month.

We insured the data met the assumptions of parametric statistical tests (Sokal and Rohlf 1995). Transformations were applied to data as necessary. In all cases where a transformation was required, natural log transformations were used. In cases where two samples were compared, if the assumption of homoscedasticity was violated, a t-test that did not assume equal variances was used. When multiple tests of the same hypothesis were conducted (e.g. microhabitat use comparisons), a Bonferroni correction was applied to the decision rule of each test (Sokal and Rohlf 1995). The significance level was set at 5%.

## Results

Water temperatures declined from fall to winter but remained several degrees above freezing throughout the winter (Figure 2). Additionally, water temperatures were quite stable throughout the winter. The lowest mean daily water temperature in the middle of the study reach was 2.8°C on 12 January 1998, and water temperature rose to 6°C by 15 February 1998.

Runs were the most common mesohabitat type in the study area, whereas pools and riffles were relatively rare (Table 1). Water depths and water velocities reflected the characteristics of each mesohabitat type. Pools had the greatest water depth and vertical relief, whereas runs had the greatest maximum and minimum water velocities. Riffles had the greatest variation in water velocity. The substrate size in pool habitat was

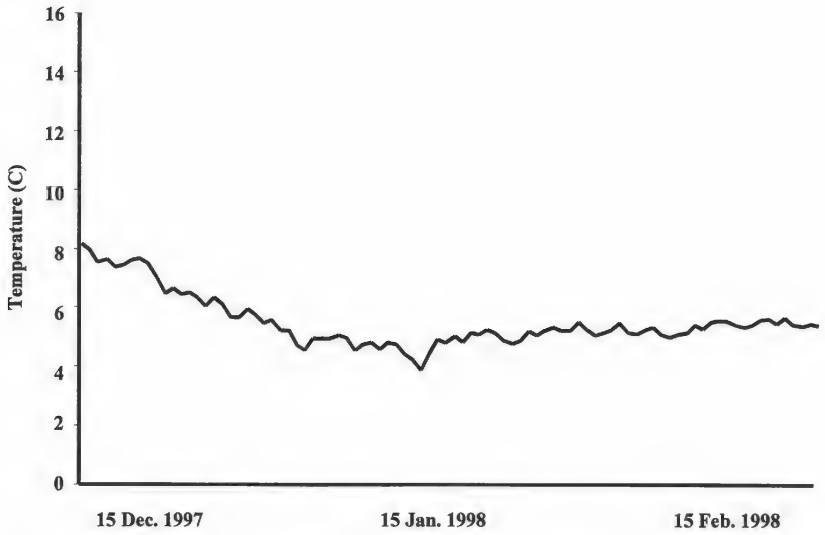


Figure 2. Mean daily water temperatures recorded in the Shoshone River during winter 1997-1998.

TABLE 1. Area of mesohabitats and average microhabitat characteristics within mesohabitats measured at 400 sampling areas along transects. Percentile values for cover refer to the percentage of sampling areas having that cover type present.

| | Mesohabitat | | |
|---|---|---|---|
| Habitat feature | Pool | Run | Riffle |
| Area (%) | 7.5 | 83.5 | 9.0 |
| Maximum depth (cm) | 161.7 | 76.5 | 23.1 |
| Minimum depth (cm) | 112.3 | 43.0 | 1.0 |
| Vertical relief (cm) | 49.7 | 33.5 | 22.4 |
| Maximum water velocity (m/s) | 0.48 | 0.82 | 0.48 |
| Minimum water velocity (m/s) | 0.27 | 0.46 | 0.10 |
| Water velocity gradient (m/s) | 0.22 | 0.36 | 0.39 |
| Mean substrate size class | 4.2 | 5.3 | 5.0 |
| Boulder cover (%) | 65.5 | 62.9 | 5.6 |
| Vegetation cover (%) | 0.0 | 2.1 | 2.8 |
| Deep water (%) | 26.7 | 2.4 | 0.0 |

on average only one size class smaller than in runs and riffles reflecting the large substrate sizes throughout the study reach.

The preponderance of large substrate was also reflected in the abundance of boulder cover (Table 1). Boulder cover was observed in over half of the sampling areas in both pools and runs and was substantially more common than aquatic vegetation or deep-water cover. Cover was infrequently observed in riffles.

Eighteen individuals from each species were tracked throughout the study. Two individuals of each species were not relocated after surgery. Fourteen cutthroat trout and 11 brown trout in pools and 14 individuals of each species in runs were observed at least five times and were included in the analysis.

Pool habitat was used by both species five to six times more frequently than would be expected if pool habitat were used in proportion to its availability. Pool habitat constituted 7.5% of the available habitat within the study area, however, 43% (SE = 10%) of cutthroat trout observations and 38% (SE = 10%) of brown trout observations were made in pools.

Both cutthroat trout and brown trout were found more frequently in runs than in pools and neither species used riffle habitat during the study. On average, 57% of cutthroat trout locations and 62% of brown trout locations were in runs, however, there was substantial variation among individuals of both species. Four cutthroat trout were found exclusively in pools, four were exclusively in runs, and 10 used both pools and runs. Similarly, four brown trout were found exclusively in pools, seven were only found in runs, and seven were observed in both pools and runs.

TABLE 2. Grand mean and range of means for microhabitat parameters measured at and estimated for fish locations in two mesohabitats in the Shoshone River.

| Habitat feature | Pool | | Run | |
|---|---|---|---|---|
| | Grand mean | Range of means | Grand mean | Range of means |
| **Cutthroat trout** | | | | |
| Maximum depth (cm) | 190.6 | 119.1-405.0 | 102.9 | 56.2-136.3 |
| Minimum depth (cm) | 88.3 | 30.4-140.2 | 52.5 | 17.1-81.4 |
| Vertical relief (cm) | 102.2 | 51.2-295.0 | 50.2 | 43.1-66.5 |
| Maximum velocity (m/s) | 0.37 | 0.25-0.57 | 0.57 | 0.38-0.79 |
| Minimum velocity (m/s) | 0.13 | 0.06-0.30 | 0.16 | 0.01-0.39 |
| Velocity gradient (m/s) | 0.25 | 0.14-0.37 | 0.41 | 0.23-0.69 |
| **Brown trout** | | | | |
| Maximum depth (cm) | 206.7 | 82.4-400.4 | 103.0 | 65.8-127.5 |
| Minimum depth (cm) | 74.9 | 19.1-151.9 | 38.3 | 0.0-67.3 |
| Vertical relief (cm) | 125.3 | 40.8-292.4 | 64.2 | 41.2-128.5 |
| Maximum velocity (m/s) | 0.42 | 0.20-0.81 | 0.68 | 0.48-0.86 |
| Minimum velocity (m/s) | 0.17 | 0.03-0.35 | 0.18 | 0.01-0.37 |
| Velocity gradient (m/s) | 0.29 | 0.14-0.60 | 0.50 | 0.30-0.38 |

Cutthroat trout and brown trout in both pools and runs used locations having similar microhabitat characteristics (Table 2). There were no significant differences between the two species with respect to microhabitat features used when in either pools or runs. Both species were consistently observed at locations that averaged 5-6 m from the stream bank.

Cover was always present at locations of both cutthroat trout and brown trout, however, there were some differences between the two species. When in pools, deep-water cover was observed at 61% of cutthroat trout locations, which was approximately double the frequency with which this cover type was observed at brown trout locations ($P = 0.02$). However, when in runs, both species used boulder cover more frequently than deep-water cover, with boulder cover present at 75% of cutthroat trout locations and 89% of brown trout locations. Boulder cover was significantly more common at brown trout locations than at cutthroat trout locations in runs ($P = 0.02$)

The movement frequencies of cutthroat trout and brown trout did not differ significantly. Thirty-seven percent of cutthroat trout observations were made at new locations (range: 10-60%), whereas 31% of brown trout observations were made at new locations (range: 12-54%). Similarly, distances moved by the two species did not differ significantly (Table 3) with the exception of January ($P = 0.001$) when the mean movement distance of cutthroat trout was greater than brown trout. Mean monthly movement distances varied considerably among individuals, particularly cutthroat trout. A greater number of cutthroat trout moved long distances. Seventeen of 18 brown trout remained within 300 m of their initial location, while five of 18 cutthroat trout moved to locations that were farther than 300 m from their initial location at some time during winter.

TABLE 3. Sample size, mean movement distance (m), and range of individual means (m) for three months for cutthroat trout and brown trout in the Shoshone River during the winter of 1997-1998.

| Month | Cutthroat trout | | | Brown trout | | |
|---|---|---|---|---|---|---|
| | N | Grand mean | Range of means | N | Grand mean | Range of means |
| December | 15 | 6.7 | 1.0-187.3 | 14 | 3.5 | 0.6-9.7 |
| January | 17 | 14.4 | 2.0-59.8 | 18 | 4.1 | 0.9-82.8 |
| February | 12 | 5.5 | 0.7-185.0 | 14 | 3.3 | 0.8-19.2 |

## Discussion

Few differences in habitat use were observed between cutthroat trout and brown trout during winter in the Shoshone River. Despite substantial differences in habitat use described through previous research on the two species, cutthroat trout and brown trout used similar habitat during winter low-flow periods in a regulated river system where both species have been introduced.

Both cutthroat trout and brown trout selected pool habitat. While only 7.5% of the study area was classified as pool habitat (Table 1), 38-43% of observations of both species were made in pools. This was five to six times greater than would be expected if both species were using pool habitat in proportion to its availability. Cunjak and Power (1986) stated that pools provide low water velocities and overhead cover in the form of deep water. This was true in the Shoshone River, where pools provided greater water depths and slower water velocities compared to runs. Brown and Mackay (1995) found that pools were the predominant habitat used by cutthroat trout during winter because water temperatures were slightly higher in pools providing protection from river ice. Water temperatures in the Shoshone River prevent river ice formation, so that avoidance of ice was not a factor in our study.

While there was selection for pools, both cutthroat trout and brown trout used runs most frequently. Within runs, we observed a wide array of stream microhabitats at individual locations. The variation in mean microhabitat characteristics and mesohabitat use among individuals of both species (Table 2) suggests that under these conditions both species are somewhat plastic in their selection of over-wintering habitat.

Both cutthroat trout and brown trout used similar microhabitats (Table 2). Both species were consistently found at locations having deeper than average water depths and slower than average water velocities. These findings are similar to those reported for other salmonid species in unnatural sympatry (Fausch and White 1981, Lohr and West 1992). Additionally, cutthroat trout and brown trout selected areas having greater than average vertical relief and water velocity gradients. However, since both species were able to use suitable overwintering habitats that provided slow water velocities and overhead cover, habitat was likely not limiting at the discharges and water temperatures we observed during 1997-1998.

The patterns of cover use we observed suggest that while both species selected areas having slower than average water velocities brown trout were more commonly associated with instream structure than cutthroat trout. Additionally, cover use by cutthroat trout appeared to vary between mesohabitats. While in pools cutthroat trout were not associated with cover structures, but structures such as boulders were frequently observed at cutthroat trout locations when they were in runs. Brown trout did not display this variation in cover use between mesohabitats, consistently displaying the high degree of affinity for cover structures as observed during other studies (Bachman 1984; Cunjak and Power 1986; Greenberg et al. 1996). While we cannot rule out interspecies interactions as a mechanism behind the contrasting cover use patterns we observed, the wealth of supporting research regarding cutthroat trout habitat preferences in allopatry (Brown and Mackay 1995) and sympatry (Nakano et al. 1992) suggests that innate differences in cover preference and the ubiquity of deep-water cover in pools allowed for a small degree of spatial segregation to occur in pool habitat.

Both cutthroat trout and brown trout remained active during the day even when water temperatures were below 5°C. We noted fluctuations in the radio transmitter signals during nearly all observations of both species that suggested that fish were active and making short-distance movements (Clapp et al. 1990; Young et al. 1997).

Given the water temperatures in the Shoshone River during winter, the habitat use patterns we observed likely indicated that fish were feeding throughout the winter. Hebdon (1999) found that cutthroat trout feed throughout the winter in the Shoshone River and we observed individuals of both species feeding during our study. Therefore, the nature of the environment in which we observed these fish resulted in a contrast with winter habitat use patterns by salmonids that have been recorded in natural-flowing streams (Heggenes et al. 1991). Chapman (1966) described food acquisition as the major factor in habitat use throughout most of the year, however, sheltering from predation and the environment takes precedence during winter. Because of the stability of the regulated river environment, cutthroat trout

and brown trout in the Shoshone River continually employed a feeding strategy even at low water temperatures.

Cutthroat trout and brown trout were found at similar distances from the bank through with winter with the exception of late February when cutthroat trout were farther from shore (Figure 3). Cutthroat trout movement away from the bank as water temperatures declined during winter has been observed in another river system (Brown and Mackay 1995), but those movements were believed to be in response to river ice formation. We did not detect variation in water temperature (Figure 2), occurrence of river ice, or changes in other habitat features that would account for this difference in late February in the Shoshone River. Additionally, we were not able to isolate these observations as statistical artifacts, therefore, the movement by cutthroat trout toward mid-channel remains unexplained.

A study that examined cutthroat trout movement in Utah classified individuals as mobile if they moved more than 300 m from their initial point of capture during a season (Hilderbrand and Kershner 2000). While the 300-m criterion was somewhat arbitrary, according to it, five of the 18 cutthroat trout we monitored would be considered mobile. Using this criterion, no brown trout were mobile. Our observation of mobile cutthroat trout during winter contrasts with the observations of Hilderbrand and Kershner (2000), who observed that ~25% of the cutthroat trout

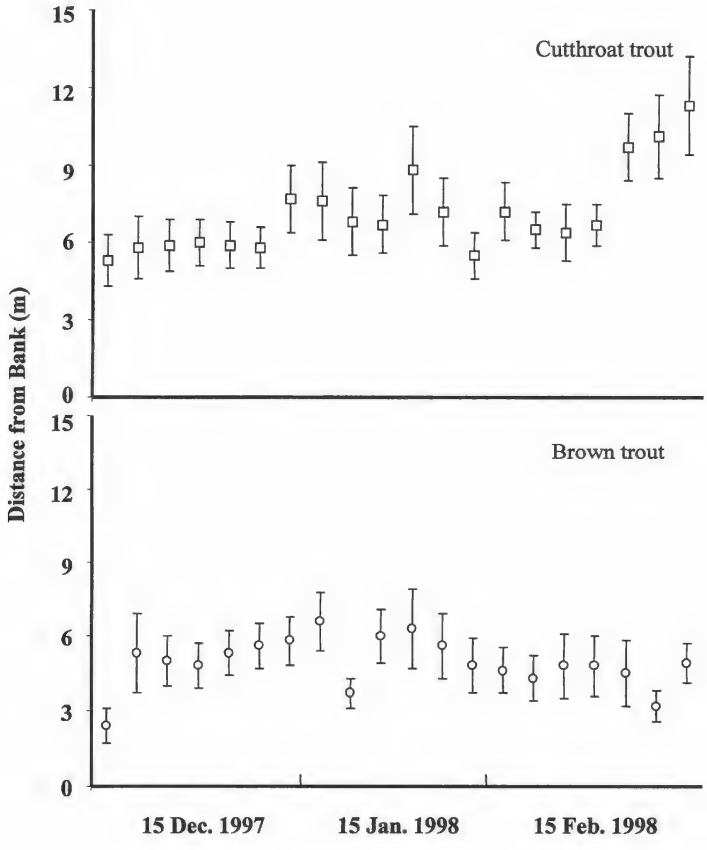


Figure 3. Average distance from the bank, ± 1 SE, for cutthroat trout and brown trout in the Shoshone River on 20 dates during the 1997-1998 winter.

population were mobile during other times of the year, but not during winter. Other studies have reported restricted cutthroat trout movement during winter (Heggenes et al. 1991). Our contrasting observations are most likely a manifestation of the differences in water temperature and environmental stochasticity between regulated and unregulated rivers during winter.

This study suggests that cutthroat trout and brown trout use a variety of similar habitats during winter when in unnatural sympatry in a regulated river system. However, winter water temperatures in the Shoshone River are substantially higher than other regulated river systems in Wyoming (Hebdon 1999) and discharge was stable during this study. The relatively benign environmental conditions that characterized the 1997-1998 winter likely contributed to a high degree of plasticity in habitat use among individuals of both species. Because of the inter-individual variation in habitat use, we observed few statistically significant differences in habitat use. Habitat segregation may be more pronounced in other regulated rivers with colder winter conditions and with less stable discharges.

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## Literature Cited

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Bidgood, B. F. 1980. Fish surgical procedure for implementation of radio tags in fish. Alberta Division of Fish and Game, Fisheries Research Board Report 20, Edmonton, Alberta.

Brown, R. S., and W. C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873-885.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. The American Naturalist 100:345-357.

Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153-176 *In* T. G. Northcote (editor), H. R. Macmillan Lectures in Fisheries. University of British Columbia - Institute of Fisheries, Vancouver, British Columbia.

Clapp, D. F., R. D. Clark Jr., and J. S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. Transactions of the American Fisheries Society 119:1022-1034.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout and brown trout. Canadian Journal of Fisheries and Aquatic Sciences 43: 1970-1981.

Dare, M. R., and W. A. Hubert. 2000. Precision and interpretation of data collected using a new measurement technique for microhabitat features at fish locations determined using radio telemetry. Journal of Freshwater Ecology 15:29-38.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout and brown trout for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Fraser, N. H. C., J. Heggenes, N. B. Metcalfe, and J. E. Thorpe. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Canadian Journal of Zoology 73:446-451.

Greenberg, L., P. Svendsen, and A. Harby. 1996. Availability of microhabitats and their use by brown trout and grayling in the River Vojman, Sweden. Regulated Rivers Research and Management 12:287-303.

Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout and cutthroat trout in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265-273.

Griffith, J. S., and R. W. Smith. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. North American Journal of Fisheries Management 13:823-830.

Haugen, T. O., and T. A. Rygg. 1996. Food- and habitat-segregation in sympatric grayling and brown trout. Journal of Fish Biology 49:301-318.

Hebdon, J. L. 1999. Prey availability, diet and body condition of sub-adult trout from fall through winter in regulated rivers, Wyoming. M. S. Thesis University of Wyoming, Laramie, Wyoming

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:757-762.

Heggenes, J., O. M. W. Krog, O. R. Lindas, J. G. Dokk, and T. Bremnes. 1993. Homeostatic behavioural responses in a changing environment: brown trout become nocturnal in winter. Journal of Animal Ecology 62:295-308.

Heidinger, R. C. 1993. Stocking for sport fisheries enhancement. Pages 309-334 *In* C. C. Kohler and W. A. Hubert (editors), Inland Fisheries Management in North America. American Fisheries Society, Bethesda, Maryland.

Hilderbrand, R. H., and J. L. Kershner. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek,

Idaho-Utah. Transactions of the American Fisheries Society 129:1160-1170.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223-235.

Lohr, S. C., and J. L. West. 1992. Microhabitat selection by brook and rainbow trout in a Southern Appalachian stream. Transactions of the American Fisheries Society 121:729-736.

Nakano, S., K. D. Fausch, T. Furukawa-Tanaka, K. Maekawa, and H. Kawanabe. 1992. Resource utilization by bull char and cutthroat trout in a mountain stream in Montana, U. S. A. Japanese Journal of Ichthyology 39:211-217.

Needhan, P. R., and A. C. Jones. 1959. Flow, temperature, solar radiation, and ice in relation to activities of fishes in Sagehen Creek, California. Ecology 40:465-474.

Pirhonen, J., J. Koskela, and M. Jobling. 1997. Differences in feeding between 1+ and 2+ hatchery brown trout exposed to low water temperature. Journal of Fish Biology 50:678-681.

Quinn, J. W., and T. J. Kwak. 2000. Use of rehabilitated habitat by brown trout and rainbow trout in an Ozark tailwater river. North American Journal of Fisheries Management 20:737-751.

Rimmer, D. M., U. Paim, and R. L. Saunders. 1983. Autumnal habitat shift of juvenile Atlantic salmon in a small river. Canadian Journal of Fisheries and Aquatic Sciences 40:671-680.

Simpkins, D. G., and W. A. Hubert. 1998. A technique for estimating the accuracy of fish locations identified by radiotelemetry. Journal of Freshwater Ecology 13:263-268.

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Simpkins, D. G., W. A. Hubert, and T. A. Wesche. 2000a. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile rainbow trout in a Wyoming tailwater. Transactions of the American Fisheries Society 129:101-118.

Simpkins, D. G., W. A. Hubert, and T. A. Wesche. 2000b. Drifting invertebrates, stomach contents, and body conditions of juvenile rainbow trout from fall through winter in a Wyoming tailwater. Transactions of the American Fisheries Society 129:1176-1184.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Freeman, New York.

Swales, S., R. B. Lauzier, and C. D. Levings. 1986. Winter habitat preference of juvenile salmonids in two interior rivers in British Columbia. Canadian Journal of Zoology 64:1506-1514.

Valdimarsson, S. K., N. B. Metcalfe, J. E. Thorpe, and F. A. Huntingford. 1997. Seasonal changes in sheltering: effect of light and temperature on diel activity in juvenile salmon. Animal Behaviour 54:1405-1412.

Wesche, T. A., C. M. Goertler, and W. A. Hubert. 1987. Modified habitat suitability index model for brown trout in southeastern Wyoming. North American Journal of Fisheries Management 7:232-237.

Wiley, R. W., R. A. Whaley, J. B. Satake, and M. Fowden. 1993. Assessment of stocking hatchery trout: a Wyoming perspective. North American Journal of Fisheries Management 13:160-170.

Young, M. K., R. A. Wilkison, J. M. P. III, and J. S. Griffith. 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. Great Basin Naturalist 57:238-244.

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# Organochlorine Pesticides, PCBs, Trace Elements and Metals in Western Pond Turtle Eggs from Oregon

## Abstract

With increased concern over the status of reptile populations globally, contaminant studies should be part of species evaluations. We analyzed eggs of western pond turtles from Fern Ridge Reservoir in western Oregon for 20 organochlorine (OC) pesticides or metabolites, 42 congener-specific polychlorinated biphenyls (PCBs), and 16 trace elements or metals. These eggs represent the first of this species analyzed. The OC pesticides and PCB residue concentrations in the western pond turtle eggs were generally low and similar to those found in eggs of snapping turtles from a remote site in Ontario, Canada. Western pond turtle eggs also contained mercury and chromium, which are metals of special concern. Although few reptilian eggs have been analyzed for metals, the 44.9 µg/g dry weight chromium in a western pond turtle egg in this study may be the highest reported in a reptilian egg. We found no significant difference in contaminant concentrations in eggs from nests in Oregon, where all turtle eggs failed to hatch compared to those where some eggs hatched. During this initial project, however, we were unable to assess fully the role of OCs, PCBs and other contaminants in the western pond turtle decline. Factors other than contaminants may be involved. In another study, snapping turtle eggs near the Great Lakes-St. Lawrence River basin were much more contaminated with evidence reported of effects on sex differentiation and reproductive endocrine function. Egg hatchability, the only reproductive parameter monitored, may not be the most sensitive endpoint. Other endpoints, including endocrine function, deformity rates, growth rates, and sex determination need study.

## Introduction

The western pond turtle (*Clemmys marmorata*) is a wide-ranging species that formerly occurred from extreme western Washington, and possibly British Columbia, to northern Baja California, mostly west of the Cascade-Sierra crest (Ernst et al. 1994). Pond turtles are now uncommon in the Willamette Valley north of Eugene, Lane Co., Oregon, but abundance in Oregon increases south of that city where temperatures are higher (Storm and Leonard 1995). Land use in the Willamette basin is 70% forested (primarily in tributary subbasins), 22% agriculture (primarily cropland on the valley floor), and 5% urbanized (Bonn et al. 1995). The basin includes 11 of the 12 largest cities in Oregon, including the 5 largest (Center for Population Research and Census 1992), and approximately 2 million people or 70% of Oregon's population (Oregon Department of Environmental Quality 1988, Bonn et al. 1995). Like other species throughout the world, the western pond turtle has experienced population declines where human numbers or disturbances have increased (Jennings and Hayes 1994, Holland 1994). The U.S. Fish and Wildlife Service was petitioned to list the species under the Endangered Species Act (U.S. Fish and Wildlife Service 1992).

The risk from contaminants in turtle habitat is potentially serious since some western pond turtle populations occur in close proximity to humans (Germano and Bury 2001). Also, since turtles spend much of their lives in or near aquatic habitats, they may be particularly vulnerable to the many contaminants that enter waterways associated with industrial and agricultural land uses. Most data on contaminants in turtles are from snapping turtles (*Chelydra serpentina*) in eastern North America (Meyers-Schöne and Walton 1994, Sparling et al. 2000) in the 1980s and 1990s. These studies revealed highly variable residue concentrations but reported regularly: p,p'-DDE (DDE), p,p'-DDT (DDT), p,p'-DDD (DDD), dieldrin, hexachlorobenzene, heptachlor epoxide, lindane, mirex, photomirex, *cis*-nonachlor, *trans*-nonachlor,

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oxychlordane, and PCBs. Polychlorinated dioxins and furans (PCDDs/PCDFs) were evaluated infrequently. Limited egg residue data were available for painted turtles (*Chrysemys picta*), box turtles (*Terrapene carolina*), and red-eared sliders (*Trachemys scripta*) (Sparling et al. 2000).

Bishop et al. (1991) reported that rates of abnormal development occurred in snapping turtle populations with the highest PCB concentrations in eggs, but rates did not correlate with OC pesticides. However, their study did not statistically consider PCDDs and PCDFs. A reanalysis of the data showed that the occurrences of abnormalities and unhatched eggs were also correlated with several PCDDs and PCDFs (Bishop et al. 1998). In snapping turtles, contaminants may also influence sex differentiation and reproductive endocrine function. The ratio of precloacal length to the posterior lobe of the plastron (PRR) is sexually dimorphic in snapping turtles, and de Solla et al. (1998) found statistically significant reductions in the PRR at three contaminated sites versus two reference sites. A significantly higher proportion of PRRs of males from a contaminated site overlapped with those of females than PRRs of males from a reference site (Lake Sasajewun). Despite changes in morphology, de Solla et al. (1998) reported few changes in 17β-estradiol or testosterone levels in blood plasma.

Since no western pond turtle eggs had been analyzed for contaminants, and contaminant-related problems were reported for other turtle species, the objectives of our study were to: (1) analyze one egg each from a series of 14 clutches from Fern Ridge Reservoir for OC pesticides and metabolites, congener-specific PCBs, and selected trace elements and metals, and (2) evaluate hatching success of eggs from each clutch in relation to residue concentrations in the sample egg collected from that clutch. Hatching success compared to egg residue concentrations on a nest basis provides a means of evaluating possible effects of contaminants on hatching (Blus 1984). When we decided to conduct contaminant studies on a series of western pond turtle eggs, only unhatched eggs were available. Thus, an evaluation of the more sensitive endpoints studied by Bishop et al. (1991) and de Solla et al. (1998) were no longer an option.

## Study Area

Fern Ridge Reservoir (ca. 7 km west of Eugene) in the southern Willamette Valley is a wide, shallow lake formed by an earth-fill dam on the Long Tom River, 37.9 km above its confluence with the Willamette River, Lane County, Oregon (Figure 1). The reservoir is drawn down in the fall and winter to provide flood-control and irrigation storage, and refilled by mid-April of each year. Approximately 1,000 ha of land around the reservoir are managed by the US Army Corps of Engineers (COE) for recreation and wildlife habitat. The major tributaries of Fern Ridge Reservoir are Coyote Creek and the Long Tom River, which together drain over 750 $km^2$ of the eastern Coast Range. The reservoir also receives flows from the Amazon Canal and several minor streams. The Amazon Canal enters the reservoir from the east, and was constructed in 1951 to divert water from Amazon Creek, which drains storm water from Eugene. When full, the reservoir has a surface area of 4,087 ha and is 7.6 m at its deepest point. Average depth is approximately 2.1 m. Emergent plants are abundant in the southern and eastern edges of the lake, along the shoreline and in coves lake-wide. Hundreds of hectares of bulrush (*Scirpus acutus*), reed canary grass (*Phalaris arundinacea*), and cattail (*Typha latifolia*) marsh are found near the mouths of the Long Tom River, Coyote Creek, and Amazon Creek.

We have studied nesting western pond turtles at Fern Ridge Reservoir since 1992. Turtles nest on the western edge of Fern Ridge Reservoir at South Applegate (Site A) and Tripass (Site B) (Figure 1). South Applegate nesting area is a 4 ha native wetland prairie in the southwest corner of the reservoir. The prairie area was plowed and grazed prior to and somewhat after the COE took ownership in 1940, and is now considered a degraded prairie community. However, native wet prairie plants, including tufted hairgrass (*Deschampsia caespitosa*), camas (*Camassia quamash* ), and rose (*Rosa nutkana*), are present. Soils are Dayton silt loam with a clay substratum, and drain poorly, which is typical of Willamette Valley wet prairie. Many turtle nest chambers in South Applegate are inundated during the winter by soils saturated with rainwater. Tripass is a 2 ha meadow dominated by short grasses and forbs near a large cove in the northwestern corner of the lake. The area was formerly farmed (pasture and hay), but is currently leased to a local school district for environmental education. The field where nesting occurs is mowed annually in late May prior to turtle nesting. The predominant soil type is Linslaw loam. Although

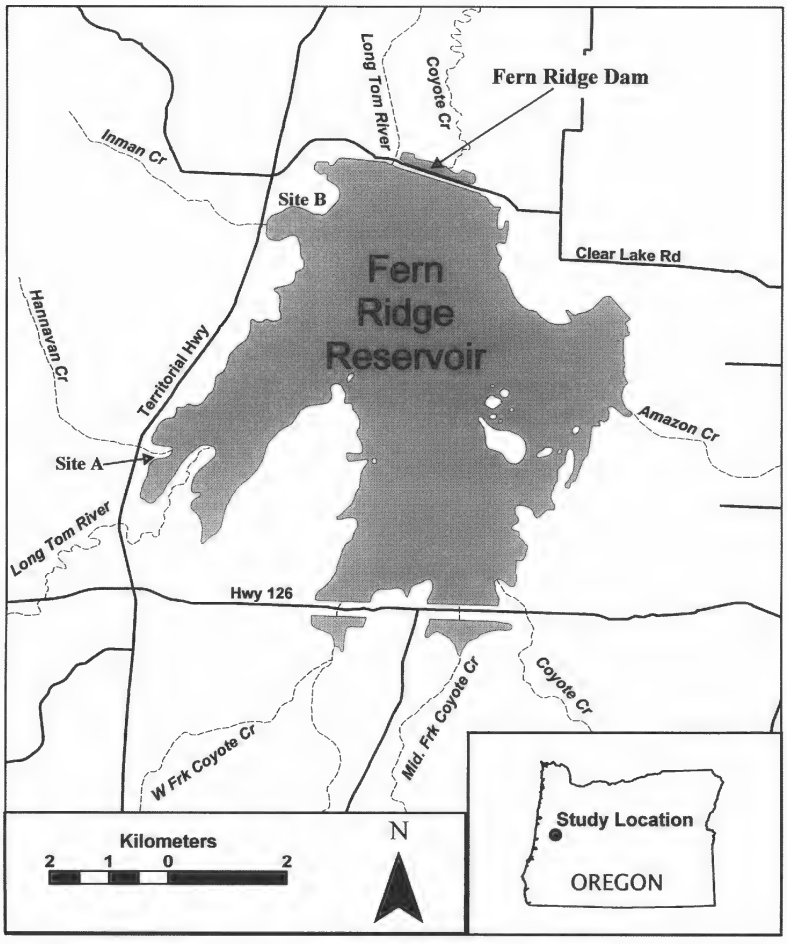


Figure 1. Fern Ridge Reservoir study areas near Eugene, Oregon with South Applegate (Site A) and Tripass (Site B) turtle nesting areas.

poorly drained, this area is less saturated than South Applegate in winter, does not support native wet prairie vegetation, and turtle nests are rarely, if ever, inundated. Turtles are frequently observed basking in the nearby cove. Evidence of turtle movement between the two sites is based upon a male turtle marked on 12 April 1996 near South Applegate that was trapped in Tripass Cove on 22 June 2000 (a distance of 4.95 km). Radio-telemetry studies of western pond turtles in western Oregon reservoirs show that trips of several kilometers along reservoir shorelines are not uncommon (Beal 1993).

## Methods

### Field Methods

Nest areas were searched daily between 1 June and 25 July 1997, and turtles nested between 4 June and 18 July. We marked 17 nests near Fern Ridge Reservoir and these were incubated in the wild. We excavated the nests on 2 October to determine egg survivorship. Most eggs had not hatched but appeared viable. Usually, successful nests have hatched by the first week of October. The unhatched eggs were taken to an incubator

at E. E. Wilson Wildlife Management Area near Corvallis, Oregon, with the hatchlings scheduled for later release as part of an experimental Head Start Program. Most clutches (14 of 17) chosen for removal had at least one intact egg that did not hatch in the incubator, and one sample egg from each of these clutches was analyzed for contaminants. The three clutches without an intact egg available for analysis included two that were successful (hatched 2 from South Applegate and hatched 9 from Tripass), and one that failed (South Applegate). The clutch sizes were 6, 11, and 9. The sample egg technique was used to evaluate residues in a sample egg in relation to hatchability of the remaining eggs in the clutch. To use the approach to evaluate critical residue concentrations, we assume that egg residue concentrations are consistent in eggs within a clutch, which has been shown for bird eggs (Blus 1984).

### Analytical Chemistry

Egg contents were weighed and placed in chemically cleaned jars. We sent egg contents to the Great Lakes Institute of Environmental Research at the University of Windsor, Windsor, Ontario, for chemical analyses. Organic chemical analyses were conducted using standard methods (Great Lakes Institute of Environmental Research 1995) to identify 20 OC pesticides and 42 PCB congeners. Data were quantified by comparing sample-peak area against standard-peak area of three standards supplied by the Canadian Wildlife Service. OC pesticides and PCB fractions were analyzed separately on an electron-capture gas chromatograph. The detection limit for OC pesticides and PCBs was 0.1 $\mu$g/kg wet weight (ww). OC pesticides and PCBs were confirmed using gas chromatography/mass spectrometry. Methodology for extraction and cleanup was checked by sample blanks, replicate samples, and certified reference samples provided by the Canadian Wildlife Service for OC pesticides and PCBs. Egg volume was determined by water displacement. We converted contents of eggs to an approximate fresh ww (for organics) using egg volume (Stickel et al. 1973). All OC and PCB residues are reported as fresh ww.

Eggs were also analyzed for metals and trace elements (Al, As, Cd, Co, Cr, Cu, Fe, K, Mg, Hg, Mn, Na, Ni, Pb, V, and Zn) by atomic absorption spectrophotometry (Great Lakes Institute of Environmental Research 1995). Dry weight (dw) detection limits ($\mu$g/g) were variable and presented with the residue data.

### Statistical Analyses

Residue concentrations were presented as geometric means and log-transformed for statistical analyses. The lower quantification limit was halved for samples in which a contaminant was not detected. This value was used to calculate geometric means when > 50% of the samples contained detectable residues. Because of unequal sample sizes, the General Linear Models Procedure (SAS Institute 1996) for analysis of variance was used. Statistical significance was $P \leq 0.05$.

## Results

### Organochlorine Pesticides and PCBs in Eggs

Variable concentrations of OC pesticides and their metabolites occurred in turtle eggs (Table 1), with DDE, oxychlordane, and *trans*-nonachlor present in all. The geometric mean for total chlordanes (*trans*-nonachlor, *cis*-nonachlor, oxychlordane, and *cis*-chlordane) was 2.32 µg/kg. Two of the three turtle eggs with the highest mirex concentrations (2.22 and 2.69 µg/kg) also contained the degradation product photomirex (0.20 and 0.30 µg/kg). PCBs measured as Aroclor 1254:1260

TABLE 1. Organochlorine contaminants (µg/kg, wet weight) in 14 western pond turtle eggs collected from Fern Ridge Reservoir, Oregon, 1997.

| Category | Geometric Mean | Range | Number of Detections |
|---|---|---|---|
| p,p'-DDE | 7.76 | 3.21-11.0 | 14 |
| Oxychlordane | 1.27 | 0.50-3.51 | 14 |
| *Trans*-nonachlor | 0.90 | 0.27-1.32 | 14 |
| Mirex | 0.36 | ND[a]-2.69 | 13 |
| Dieldrin | 0.19 | ND-0.38 | 11 |
| Heptachlor epoxide | 0.13 | ND-0.34 | 11 |
| *Cis*-Nonachlor | 0.08 | ND-0.18 | 12 |
| 1,2,4,5-TCB | NC[b] | ND-0.36 | 7 |
| Hexachlorobenzene | NC | ND-0.13 | 4 |

Note: Pentachlorobenzene; octachlorostyrene; alpha, beta and gamma hexachlorocyclohexane; 1,2,3,4-TCB (tetrachlorobenzene); *trans*-chlordane; p,p'-DDD; and p,p'-DDT were not detected. Photomirex was detected in 2 eggs (0.20 and 0.30 µg/kg) and *cis*-chlordane in 1 egg (0.09 µg/kg).

[a] ND = Not detected.

[b] NC = Not calculated if 50% or more of samples were below detection limit.

TABLE 2. Total PCBs and PCB congeners (µg/kg, wet weight) in 14 western pond turtle eggs collected from Fern Ridge Reservoir, Oregon, 1997.

| IUPAC Numbers | Geometric Mean | Range | Number of Detections | IUPAC Numbers | Geometric Mean | Range | Number of Detections |
|---|---|---|---|---|---|---|---|
| 153 | 4.96 | 1.05-10.4 | 14 | 52 | 0.33 | ND-0.78 | 11 |
| 138 | 2.93 | 0.71-3.86 | 14 | 206 | 0.32 | 0.10-0.63 | 14 |
| 180 | 2.90 | 0.50-6.35 | 14 | 195 | 0.19 | ND-0.43 | 13 |
| 118 | 2.27 | 0.47-3.99 | 14 | 171 | 0.17 | ND-0.25 | 13 |
| 179/190 | 1.22 | 0.19-2.82 | 14 | 158 | 0.13 | ND-0.23 | 12 |
| 183 | 0.72 | 0.19-1.36 | 14 | 101 | 0.12 | ND-0.32 | 10 |
| 203 | 0.58 | 0.13-1.24 | 14 | 146 | 0.11 | ND-0.13 | 13 |
| 99 | 0.55 | 0.19-0.75 | 14 | 149 | 0.08 | ND-0.25 | 8 |
| 182/187 | 0.51 | 0.20-0.69 | 14 | 200 | NC[b] | ND-0.20 | 7 |
| 194 | 0.45 | 0.14-0.98 | 14 | 66/95 | NC | ND-0.43 | 4 |
| 105 | 0.42 | ND[a]-1.15 | 13 | $\Sigma$ Congeners | 19.8 | 4.78-37.1 | 14 |
| 201 | 0.33 | 0.08-0.55 | 14 | Aroclor 1254:1260 | 39.6 | 9.57-52.1 | 14 |

Note: IUPAC 31/28, 42, 64, 74, 70, 60, 97, 87, 151, 141, 129, 185, and 174 were not detected.

PCBs only present in one egg (IUPAC 49, 0.26 µg/kg; IUPAC 44, 0.11 µg/kg; IUPAC 110, 0.09 µg/kg; IUPAC 172, 0.07 µg/kg).

[a] ND = Not detected.

[b] NC = Not calculated if 50% or more of samples were below detection limit.

TABLE 3. Trace elements and metals (µg/g, dry weight) in 14 western pond turtle eggs from Fern Ridge Reservoir, Oregon, 1997.

| Nest Number | Chromium | Copper | Iron | Potassium | Magnesium | Manganese | Sodium | Nickel | Zinc | Mercury |
|---|---|---|---|---|---|---|---|---|---|---|
| A-1 | 7.20 | 36.2 | 138 | 5910 | 1020 | 2.28 | 7040 | 8.59 | 58.7 | ND[a] |
| A-2 | ND | 4.39 | 62.1 | 4560 | 1040 | 1.45 | 5310 | 2.62 | 52.1 | 0.26 |
| A-6 | 3.72 | 5.26 | 110 | 6450 | 1160 | 2.51 | 7300 | 5.59 | 67.7 | ND |
| A-7 | 6.84 | 5.33 | 98.8 | 5960 | 937 | 5.25 | 7310 | 7.97 | 43.5 | ND |
| A-8 | 4.61 | 7.18 | 120 | 6310 | 1460 | 2.29 | 8020 | 6.11 | 71.7 | 0.27 |
| A-9 | ND | 5.89 | 72.8 | 6610 | 1430 | 2.15 | 7470 | 1.30 | 72.6 | ND |
| A-10 | ND | 5.35 | 57.3 | 5860 | 917 | 0.81 | 5740 | 0.70 | 51.8 | ND |
| A-13 | ND | 5.34 | 62.1 | 5530 | 850 | 1.19 | 5810 | 1.41 | 59.9 | ND |
| A-14 | 4.03 | 9.46 | 86.2 | 9720 | 1060 | 3.66 | 12200 | 0.60 | 100 | ND |
| A-15 | ND | 6.36 | 60.3 | 6360 | 579 | 1.93 | 8160 | 1.48 | 60.5 | ND |
| A-16 | 44.9 | 77.0 | 325 | 6360 | 698 | 4.71 | 6930 | 27.7 | 74.5 | ND |
| B-2 | ND | 5.98 | 57.0 | 7270 | 1070 | 1.18 | 7700 | 0.56 | 45.2 | 0.35 |
| B-4 | ND | 6.67 | 85.3 | 7650 | 1240 | 2.97 | 10500 | 1.88 | 94.5 | 0.54 |
| B-5 | ND | 4.86 | 86.2 | 5390 | 981 | 2.85 | 8070 | 1.07 | 87.5 | ND |
| Geometric Mean | NC[b] | 8.05 | 89.3 | 6330 | 1000 | 2.22 | 7510 | 2.41 | 65.1 | NC |
| Detection Limit | 2.00 | 2.00 | 1.00 | 16.0 | 1.00 | 0.05 | 3.00 | 0.50 | 0.50 | 0.25 |

Note: Cobalt found above detection limit (0.30 µg/g) in only one egg (A-16, 0.60 µg/g). Aluminum (4.00), Arsenic (2.00), Cadmium (0.10), Lead (1.50) and Vanadium (1.50) were not found above the detection limits listed here.

[a] ND = Not detected.

[b] NC = Not calculated if 50% or more of samples were below the detection limit.

were present in all turtle eggs and at higher concentrations (39.6 µg/kg) than any of the OC pesticides (Table 2). The dominant PCBs found in the eggs were International Union of Pure and Applied Chemistry [IUPAC] numbers 153, 138, 180 and 118 (Table 2).

## Metals and Trace Elements in Eggs

Of special interest are the nonessential elements cadmium, lead, and mercury, but also chromium which is an essential nutrient in the trivalent form ($Cr^{+3}$) but toxic in the hexavalent form ($Cr^{+6}$) (Table 3). Cadmium and lead do not readily accumulate

in eggs and were not detected in the eggs collected during this study, whereas mercury was detected in 4 of 14 eggs (Table 3). Chromium (form unknown) was detected in 6 of 14 eggs collected. Interactions among metals are common and may be either beneficial or harmful. For example, A-1 and A-16 with the highest chromium concentrations also contained the highest copper, iron, and nickel. Other eggs with chromium detected (A6, A7, A8, and A14) often had copper, iron, and nickel concentrations above the geometric mean.

### Egg Residues and Hatchability

Knowledge of the eggs that hatched in the incubator and in the field provide some insight into possible effects of egg residue concentrations on overall hatchability. Unfortunately, 14 nests is a small number for a rigorous statistical assessment. The success or failure of the 14 individual clutches varied widely, but the OC pesticides, PCBs and most metal concentrations were within a relatively narrow range (Tables 1-3). The success of the 14 nests (at least one egg hatched in 57.1% of the nests, and 21.1% of the eggs hatched) was low (Table 4), but with the three nests added where no eggs were available for analysis, the percentages (based on 17 nests) were slightly higher (58.8% of the nests successful, and 25.2% of eggs hatched). With no significant difference in the geometric means for DDE, total PCBs, oxychlordane, *trans*-nonachlor, *cis*-nonachlor, mirex, heptachlor epoxide, and dieldrin in eggs from nests that were successful (hatched at least one egg) versus eggs from nests that totally failed, and the incidence of mercury and chromium (and the extreme values) higher in the sample eggs representing successful clutches, we found no evidence of adverse effects on hatchability related to 10 contaminants (Table 4). The 7-egg clutch with the highest chromium concentration (44.9 µg/g dw) was successful with one egg hatched.

## Discussion

Western pond turtles nesting near Fern Ridge Reservoir were exposed to a series of contaminants as evidenced by residue concentrations found in their eggs. However, we were limited in our ability to evaluate possible effects of these contaminants because eggs from only 14 nests were studied. Reproductive success was generally low in 1997, but no obvious relationship between

TABLE 4. Comparison of residue concentrations and hatchability of eggs (in field and incubator) from western pond turtles collected at Fern Ridge Reservoir, 1997.

| | Mean (Range) | | Geometric Mean µg/kg wet weight (Extreme) | | | | | | | Occurrence (Extreme µg/g dry weight) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nests (N) | Clutch Size | Young Hatched | DDE | Total PCBs[a] | OXY[a] | TRNO[a] | CSNO[a] | Mirex[a] | HE[a] | DIEL[a] | Mercury[b] | Chromium[b] |
| Failed[c] (6) | 7.50 (5-10) | 0 | 7.48 (10.81) | 35.22 (52.14) | 1.01 (1.56) | 0.74 (1.14) | 0.07 (0.11) | 0.22 (2.22) | 0.12 (0.17) | 0.17 (0.24) | 1 (0.35) | 2 (6.84) |
| Successful[d] (8) | 8.00 (5-12) | 2.88 (1-8) | 7.98 (10.99) | 43.32 (51.93) | 1.51 (3.51) | 1.04 (1.32) | 0.08 (0.18) | 0.54 (2.69) | 0.14 (0.34) | 0.21 (0.38) | 3 (0.54) | 4 (44.9) |
| Combined[e] (14) | 7.79 (5-12) | 1.64 (0-8) | 7.76 | 39.64 | 1.27 | 0.90 | 0.08 | 0.36 | 0.13 | 0.19 | 4 | 6 |

Note: No statistically significant difference was found in residue concentrations (geometric means) from eggs collected at failed versus successful nests.

[a] Total PCBs (Aroclor 1254:1260), OXY (oxychlordane), TRNO (*trans*-nonachlor), CSNO (*cis*-nonachlor), HE (heptachlor epoxide), DIEL (dieldrin).

[b] Number eggs with detectable concentrations.

[c] No eggs hatched.

[d] At least one egg hatched.

[e] For 17 nests studied (including 3 nests with no eggs analyzed) mean clutch size 7.94 eggs, mean young hatched 2.00.

residue concentrations and hatchability of eggs was found. Perhaps the most meaningful residue comparisons with our data are comparisons with the large series of snapping turtle eggs collected in 1989-91 from the Great Lakes–St. Lawrence River basin (Bishop et al. 1998), although we must recognize that species sensitivity to contaminants may vary. Eggs were collected at one remote reference site (Lake Sasajewun, Algonquin Provincial Park) and eight other sites in areas of concern because of environmental contamination and habitat loss. Organochlorine pesticides and PCB residue concentrations in the western pond turtle eggs from Oregon were low and similar to the snapping turtle data from the remote site at Algonquin Provincial Park, but much lower than all other sites where contaminant-related problems were encountered (Bishop et al. 1998).

Bonin et al. (1995) reported PCB congener composition between snapping turtles and mudpuppies (*Necturus maculosus*) along the St. Lawrence and Ottawa Rivers. In snapping turtle eggs, three congeners (118, 138 and 153) constituted over half of the total PCB concentration. These congeners were also dominant in mudpuppy tissues, but they represented only one-third of the PCBs. Bishop et al. (1996) reported that snapping turtle and herring gull (*Larus argentatus*) eggs had a similar PCB composition pattern. Western pond turtle eggs at Fern Ridge Reservoir also had the same three congeners constituting a similar 51.4% of the total PCB concentration. Bonin et al. (1995) noted that despite differences in the physiology of endotherms such as birds and ectotherms such as reptiles, their studies suggest that the metabolic capacities for detoxification of chlorinated hydrocarbons are similar.

Few metals and trace elements have been analyzed in turtle eggs. The highest chromium value in this study (44.9 µg/g dw) was considerably higher than the 1.2 µg/g ww (perhaps 4.8-6 µg/g dw) extreme for reptilian eggs in an American alligator (*Alligator mississippiensis*) from Florida (Heinz et al. 1991). Interactions among metals also seem apparent, but are poorly understood. Mercury was significantly higher in eggs of the omnivorous snapping turtle than in the sympatric but predominantly herbivorous red-eared slider (Meyers-Schöne 1989, Meyers-Schöne et al. 1993). The western pond turtle is a dietary generalist feeding mostly on vegetation, invertebrates, and, rarely, vertebrates (small fish, tadpoles) (Bury 1986). Thus, much as in birds, differences in contaminant concentrations in turtles seem to reflect the trophic level of the diet.

Our findings regarding contaminants from this study must be considered preliminary because (1) many contaminants were not evaluated, (2) some metals which do not readily accumulate in eggs (undetected or in low concentrations) may concentrate and cause damage elsewhere in the turtles, and (3) the evaluation of more sensitive endpoints like endocrine function, deformity rates, growth rates, and sex ratios was not an option. Embryonic exposure of low-dose pesticides (chlordane, *trans*-nonachlor, DDE) given to red-eared sliders altered expected sex outcomes and hatchling steroid physiology (Willingham 2001). These changes can certainly affect an organism's fitness and the same contaminants were found in turtle eggs from Oregon. One of the first records of wild birds killed by chlordane occurred near Corvallis, although most chlordane uses were banned by 1980 (Blus et al. 1983). More research on contaminants, patterned after snapping turtle studies in Canada, needs to be conducted on turtles in Oregon and other western areas. Nondestructive sampling techniques, including blood samples and tail clips, have been suggested for sampling threatened reptile species (Hopkins et al. 2001). Field studies of turtles are further limited by a poor understanding of relationships between most contaminants and turtle responses, but increased concern over the status of reptile populations has stimulated the demand for assessments of contaminant effects on populations. We acknowledge, however, that factors other than contaminants may be involved in the population decline.

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## Literature Cited

Beal, K. 1993. Western pond turtle report. Trapping and telemetry results and analysis, Fall Creek and Lookout Point Reservoirs. Unpublished Report to US Army Corps of Engineers, Willamette Valley Projects Office, Lowell, Oregon.

Bishop, C. A., R. J. Brooks, J. H. Carey, P. Ng, R. J. Norstrom, and D. R. S. Lean. 1991. The case for a cause-effect linkage between environmental contamination and

development in eggs of the common snapping turtle (*Chelydra serpentina*) from Ontario, Canada. Journal of Toxicology and Environmental Health 33:512-547.

Bishop, C. A., P. Ng, R. J. Norstrom, and K. E. Pettit. 1996. Temporal and geographic variation of organochlorine residues in eggs of the common snapping turtle (*Chelydra serpentina serpentina*) (1981-1991) and comparisons to trends in the herring gull (*Larus argentatus*) in the Great Lakes Basin in Ontario, Canada. Archives of Environmental Contamination and Toxicology 31:512-524.

Bishop, C. A., P. Ng, K. E. Pettit, S. W. Kennedy, J. J. Stegeman, R. J. Norstrom, and R. J. Brooks. 1998. Environmental contamination and developmental abnormalities in eggs and hatchlings of the common snapping turtle (*Chelydra serpentina serpentina*) from Great Lakes & St. Lawrence River basin. Environmental Pollution 101:143-156.

Blus, L. J. 1984. DDE in birds' eggs: comparison of two methods for estimating critical levels. Wilson Bulletin 96:268-276.

Blus, L. J., O. H. Pattee, C. J. Henny, and R. M. Prouty. 1983. First records of chlordane-related mortality in wild birds. Journal of Wildlife Management 47:196-198.

Bonin, J., J-L. DesGranges, C. A. Bishop, J. Rodrigue, A. Gendron, and J. E. Elliott. 1995. Comparative study of contaminants in the mudpuppy (Amphibia) and the common snapping turtle (Reptilia), St. Lawrence River, Canada. Archives of Environmental Contamination and Toxicology 28:184-194.

Bonn, B. A., S. R. Hinkle, D. A. Wentz, and M. A. Uhrich. 1995. Analysis of nutrient and ancillary water-quality data for surface and ground water of the Willamette Basin, Oregon, 1980-90. U.S. Geological Survey Water-Resources Report 95-4036.

Bury, R. B. 1986. Feeding ecology of the turtle *Clemmys marmorata*. Journal of Herpetology 20:515-521.

Center for Population Research and Census. 1992. Population estimates for Oregon 1980-81. Portland State University, Portland, Oregon.

de Solla, S. R., C. A. Bishop, G. Van Der Kraak, and R. J. Brooks. 1998. Impact of organochlorine contamination on levels of sex hormones and external morphology of common snapping turtles (*Chelydra serpentina serpentina*) in Ontario, Canada. Environmental Health Perspectives 106:253-268.

Ernst, C. H., J. E. Lovich, and R. W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution, Washington, D. C.

Germano, D. J., and R. B. Bury. 2001. Western pond turtles (*Clemmys marmorata*) in the Central Valley of California: status and population structure. Transactions of the Western Section of the Wildlife Society. 37:22-36.

Great Lakes Institute for Environmental Research. 1995. Methods and Procedures Quality Manual, First Edition, 0 Revision, University of Windsor, Windsor, Ontario, Canada.

Heinz, G. H., H. F. Percival, and M. L. Jennings. 1991. Contaminants in American alligator eggs from Lake Apopka, Lake Griffin, and Lake Okeechobee, Florida. Environmental Monitoring and Assessment 16:277-285.

Holland, D. C. 1994. The western pond turtle: habitat and history. Unpublished Final Report. DOE/BP-62137-1. Bonneville Power Administration, U.S. Department of Energy, and Wildlife Diversity Program, Oregon Department of Fish and Wildlife, Portland, Oregon.

Hopkins, W. A., J.S. Roe, J. W. Snodgrass, B. P. Jackson, D. E. Kling, C. L. Rowe, and J. D. Congdon. 2001. Nondestructive indices of trace element exposure in squamate reptiles. Environmental Pollution 115:1-7.

Jennings, M. R., and M. P Hayes. 1994. Amphibian and reptile species of special concern in California. Unpublished Final Report. California Department of Fish and Game, Contract No. 8023, Rancho Cordova, California.

Meyers-Schöne, L. 1989. Comparison of two freshwater turtle species as monitors of environmental contamination. Ph.D. Dissertation, University of Tennessee, Knoxville, Tennessee.

Meyers-Schöne, L., and B. T. Walton. 1994. Turtles as monitors of chemical contaminants in the environment. Reviews Environmental Contamination and Toxicology 135:93-153.

Meyers-Schöne, L., L. R. Shugart, J. J. Beauchamp, and B. T. Walton. 1993. Comparison of two freshwater turtle species as monitors of radionuclide and chemical contamination: DNA damage and residue analysis. Environmental Toxicology and Chemistry 12:1487-1496.

Oregon Department of Environmental Quality. 1988. Oregon Environmental Atlas. Portland, Oregon.

SAS Institute. 1996. SAS user's guide: statistics. Version 6.12 Edition, SAS Institute, Inc., Cary, North Carolina.

Sparling, D. W., G. Linder, and C. A. Bishop (editors). 2000. Ecotoxicology of Amphibians and Reptiles. Society of Environmental Toxicology and Chemistry. Pensacola, Florida.

Stickel, L. F., S. N. Wiemeyer, and L. J. Blus. 1973. Pesticide residues in eggs of wild birds: adjustment for loss of moisture and lipid. Bulletin Environmental Contamination and Toxicology 9:193-196.

Storm, R. M., and W. P. Leonard (editors). 1995. Reptiles of Washington and Oregon. Seattle Audubon Society, Seattle, Washington.

U. S. Fish and Wildlife Service. 1992. 90-day finding and commencement of status reviews for a petition to list the western pond turtle and California red-legged frog. Federal Register 57:45761.

Willingham, E. 2001. Embryonic exposure to low-dose pesticides: effects on growth rate in the hatchling red-eared slider turtle. Journal of Toxicology and Environmental Health (A) 64:257-272.

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# Using GIS to Guide Field Surveys for Timberline Sparrows in Northwestern Montana

## Abstract

For many species, we lack the basic information on distribution and abundance that is needed for conservation and management. The timberline Brewer's sparrow, a migratory songbird previously known to breed only in the Canadian and Alaskan Rockies, was recently discovered in abundance in high-elevation areas of Glacier National Park, Montana. Because the southern limit of this subspecies' breeding range was unknown, we developed a GIS-based model to predict timberline sparrow habitat along the Rocky Mountain front south of Glacier National Park. We field-tested the model by surveying 40 predicted sites in the Lewis and Clark National Forest. We found suitable habitat at 20 of the 40 sites (50%), and timberline sparrows were present at 4 of these; we also found timberline sparrows at one site that was not predicted. The discovery of nesting birds at Jones Creek, in the Teton River drainage, extends the known breeding range of this subspecies 50 km south. Our study indicates that, even with relatively few initial data, GIS can be successfully used as a tool to guide surveys for rare species. However, there are inherent limitations in models built with restricted data, and species' distributions can be driven by factors not readily modeled in a GIS. Therefore, GIS models often must be treated as working hypotheses, to be tested and improved as additional data become available.

## Introduction

Effective conservation and management of populations is impossible without detailed knowledge of a species' range, abundance, and habitat associations. Yet we often lack this basic information for species that inhabit inaccessible environments or have specialized habitat requirements, and for those that occur as fragmented populations or at relatively low densities (Rimmer et al. 1996). In recent years, geographic information systems (GIS) have made it possible to model habitat associations over large geographic areas. Researchers use satellite imagery and other digital data sources to quantify vegetative and topographic features correlated with a species' presence in one area, then extrapolate these data using a GIS to predict similar habitat in adjacent areas (Clark et al. 1993, Andries et al. 1994, Hepinstall and Sader 1997, Skidmore 1998). Thus, it may be possible to use GIS models to predict the potential distribution of rare or poorly known species.

The timberline subspecies of the Brewer's sparrow *(Spizella breweri taverneri)* is an excellent candidate for using this approach. First, this subspecies' high-elevation breeding habitat is relatively inaccessible, and consequently, details of its distribution are poorly understood. Timberline sparrows breed at scattered sites in the Canadian Rockies between southeastern Alberta and Alaska, but it is not known if this distribution is continuous because few surveys have been conducted in the region (Klicka et al. 1999, Rotenberry et al. 1999). Recently, timberline sparrows were found breeding in abundance in Glacier National Park east of the Continental Divide, and several breeding sites were adjacent to the southern boundary of the park (Walker 1999). Therefore, the limit of the breeding range of this subspecies may extend farther south. In Montana, several mountain ranges with treeline habitat may support timberline sparrows. It has previously been suggested that populations may exist in Montana and in other parts of the northwestern United States (Griscom 1928, Grinnell et al. 1930, Grinnell 1932, McTaggart-Cowan 1946).

Second, timberline sparrows appear to have narrow habitat requirements. Throughout their range, they are consistently found in dense, krummholz

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shrubs at treeline. This potentially simplifies the process of modeling suitable habitat. Third, timberline sparrows may become a conservation concern in the near future. Although the timberline sparrow is currently listed as a subspecies of the Brewer's sparrow *(Spizella breweri)* (American Ornithologists' Union 1998), recent genetic, behavioral, and morphological data suggest that it may warrant full species status (Klicka et al. 1999, 2001; but see Mayr and Johnson 2001). If the timberline sparrow is recognized as a distinct species, it may merit future attention from conservationists. The krummholz vegetation preferred by timberline sparrows is thought be particularly sensitive to climate change (Hessl and Baker 1997, Lloyd and Graumlich 1997, Peteet 2000), suggesting that habitat availability may change in the coming years.

Surveys of rugged, high-elevation sites in the northern Rockies are logistically difficult, thus it may be more efficient to use GIS to identify likely timberline sparrow habitat and to guide survey efforts. Therefore, the objectives of this study were: 1) to test the usefulness of a GIS model for locating potential timberline sparrow habitat; and 2) to investigate the distribution, abundance, and breeding status of this subspecies south of its recorded range in northwestern Montana.

## Methods

### Study Species' Habitat Use

Although the species composition of timberline sparrow breeding habitat varies across its range, this subspecies has consistently been found in krummholz shrubs or conifers at upper treeline. In Canada and Alaska, timberline sparrows nest in clumps of dwarf spruce (*Picea* spp.), subalpine fir (*Abies lasiocarpa*) (McTaggart-Cowan 1946), and dwarf birch (*Betula nana*) (Swarth 1926) on otherwise open slopes, or in patches of stunted willow (*Salix* spp.) surrounded by an understory of dwarf birch (Doyle 1997). In Glacier National Park, Walker (1999) found them in small, isolated patches of krummholz subalpine fir on open slopes and ridges of alpine tundra or talus (Figure 1). The single feature common to all locations is the presence of patchy krummholz shrubs. Therefore, our primary goal in building the GIS model was to predict areas of low, patchy krummholz at or near treeline.

## Study Area

Our study region in northwestern Montana encompassed the Flathead (FNF) and Lewis and Clark (LCNF) National Forests, and a 5 km surrounding

Figure 1. Habitat in Glacier National Park, where timberline sparrows (*Spizella breweri taverneri*) were found in small, isolated patches of krummholz subalpine fir on open slopes and ridges of alpine tundra or talus.

buffer zone (Figure 2). The southeast corner of the Scapegoat Wilderness Area was excluded because satellite data were not available. We restricted our surveys to the east side of the Continental Divide, where timberline sparrows had been previously found in Glacier NP (Walker 1999).

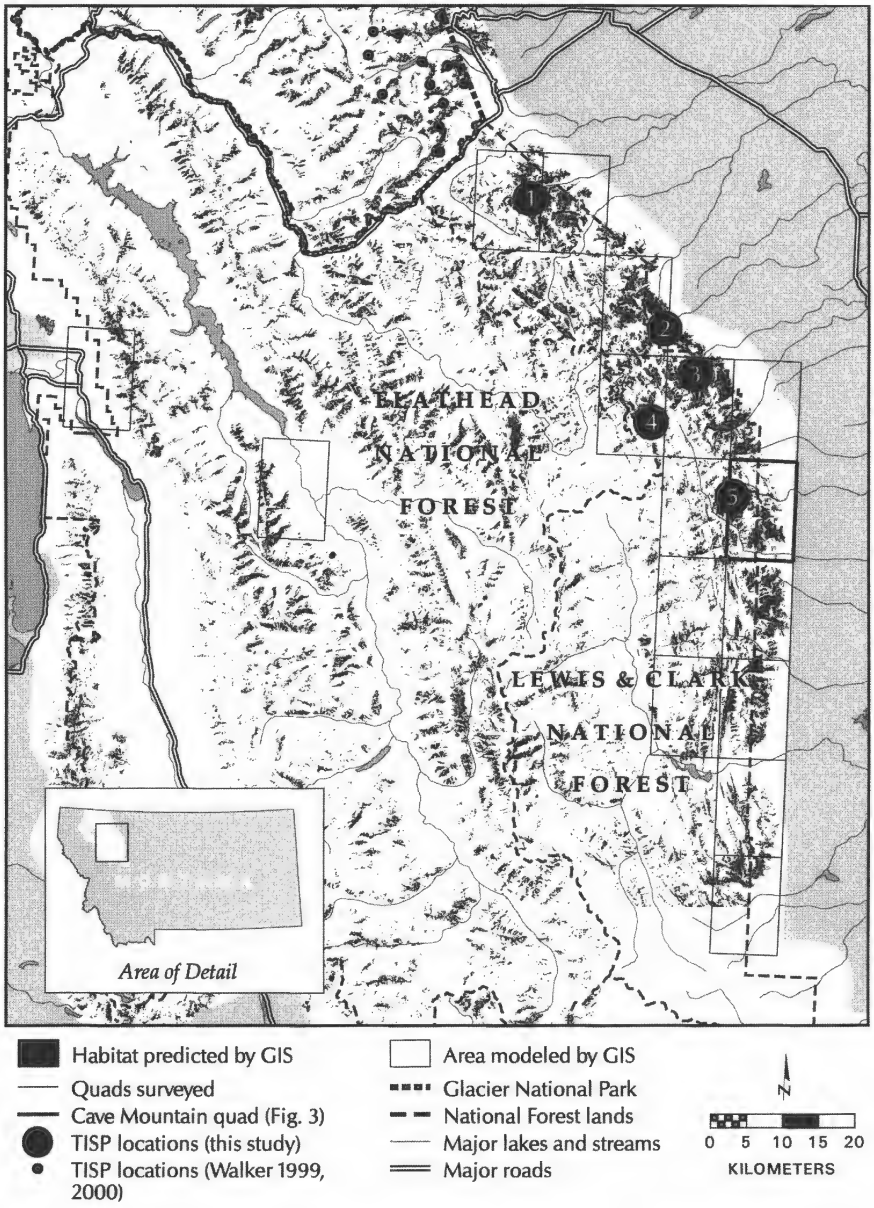


Figure 2. Study area in northwestern Montana, encompassing the Flathead and Lewis and Clark National Forests. Habitat was classified for a larger area than shown on this map (see inset), which focuses on the area where surveys were conducted. Timberline sparrows (TISP) were found at five locations: 1) Mount Baldy; 2) Swift Reservoir; 3) Sheep Creek; 4) Crazy Creek; and 5) Jones Creek.

We assumed that the vegetation, climate, and topography would be similar in both regions, making the east side of the LCNF the most likely place to find new populations. Moreover, access to sites on the west side of the Continental Divide is extremely difficult.

## The GIS Model

Our modeling approach was in large part dictated by limited data and by a narrow window of time before the onset of the 1999 field season. Rather than attempting to define timberline sparrow habitat based on land cover, a derived GIS layer, we instead used satellite imagery and digital elevation, layers from which land cover itself might be mapped, in relation to existing timberline sparrow survey data to create a habitat map (sensu Aspinall and Veitch 1993, Hepinstall and Sader 1997). Land cover maps at appropriate spatial and thematic resolutions are not always available; nor are they necessarily developed with the habitat requirements of a given wildlife species in mind, meaning that the relationship between land cover classes and habitat for that species may not be accurate (Hepinstall and Sader 1997). By working directly with satellite imagery and elevation, both readily available, we sought to avoid this potential source of error. The outputs of our process were two GIS layers, one predicting sparrow presence or absence (and thus presumably the presence of suitable habitat), and the other documenting the probability that those predictions were correct.

GIS analyses were conducted using ArcInfo software (ESRI 1998) on an IBM RS/6000 workstation. Analyses were conducted across 23,418 $km^2$ in northwestern Montana, including the study region and much of Glacier NP, where observations for timberline sparrows had been previously collected and made available for model development. The primary data inputs were presence-absence points from field surveys in Glacier NP in 1998 and early 1999 (Walker 1999, 2000), Landsat Thematic Mapper (TM) satellite imagery, and digital elevation data. The latter two were at 30 m resolution. We imported the UTM coordinates for Glacier NP survey points into ArcInfo, assigning each location a 1 or 0 value to denote timberline sparrow presence or absence. In spring 1999, we added additional, unsurveyed absence points to represent areas with obviously unsuitable habitats (e.g., alpine tundra, low-elevation forest) to reduce the likelihood of mapping such areas as predicted habitat.

We assembled satellite imagery for the study area from TM scenes P41/R26, P41/R27, P40/R26, and P40/R27. A histogram-matching technique that matched the four TM scenes to each other was used to adjust for such differences as image acquisition date and atmospheric conditions. The resulting composite image, like the input TM scenes, had seven channels of data, each with potential values ranging from 0-255. After some experimentation, channels 3, 4, and 5 were selected to classify timberline sparrow habitat. These channels are commonly used to classify vegetation in northern forested regions (Horler and Ahern 1986, Frank 1988, Bolstad and Lillesand 1992) and were most promising for classifying habitat based on the proportion of timberline sparrow locations that they correctly classified. An elevation layer was compiled from USGS 7.5-minute digital elevation models, and then scaled so that its values ranged from 0-255 to match the satellite imagery. The classification process was exploratory and iterative; only the final output used to make field maps is described here.

Once the input layers had been assembled, we classified potential habitat. First, field locations were overlaid with four variables: TM channels 3, 4, and 5, and scaled elevation. We used a bootstrap procedure (Steele et al. 1998) to test how well each plot could be classified by all the other plots in the dataset. Twenty-one plots with 0% probability of correct classification were identified and deleted from the original dataset, leaving 194 plots where birds were absent and 60 plots where birds were present. Deleting these 21 plots brought overall accuracy up from 85% (95% for absence, 57% for presence) to 93% (98% for absence, 74% for presence). Based on the four variables above and the reduced set of 254 plots, the ArcInfo CLASSSIG function was used to calculate covariance matrices and means for the two classes (presence/absence), and the results were written to a signature file (Table 1). Using the data from this signature file, the ArcInfo MLCLASSIFY function was used to perform a maximum-likelihood classification of TM channels 3, 4, and 5, and scaled elevation. An output GIS layer was produced that had values of 1 and 0, predicting either timberline sparrow presence or absence. A second output layer contained information on the probability of correct classification.

TABLE 1. Covariance matrices (a) and means (b) for the three spectral classes (Landsat Thematic Mapper (TM) channels 3, 4, and 5) and one elevation GIS layer used to predict timberline sparrow habitat, taken from a signature file produced by the ArcInfo CLASSSIG function. Elevation values were scaled to match the range of values in the TM imagery (0-255). Values of these parameters where sparrows were absent (n = 194) are at left and where sparrows were present are at right (n=60).

| | Sparrow absent | | | | Sparrow present | | | |
|---|---|---|---|---|---|---|---|---|
| | TM3 | TM4 | TM5 | ELE | TM3 | TM4 | TM5 | ELE |
| a. TM3 | 223.85 | 78.13 | 409.54 | 288.90 | 38.25 | –4.38 | 80.17 | 66.66 |
| TM4 | | 406.20 | 288.34 | –74.03 | | 125.09 | 61.09 | 20.64 |
| TM5 | | | 1118.43 | 456.49 | | | 256.85 | 148.57 |
| ELE | | | | 881.17 | | | | 271.16 |
| b. | 26.48 | 57.58 | 67.59 | 131.90 | 30.55 | 77.83 | 94.03 | 123.70 |

We then generated field maps of predicted timberline sparrow habitat for 16 7.5-minute quadrangles (Figure 2). Figure 3 shows a sample map for the Cave Mountain quadrangle. Only areas with ≥50% likelihood of correct classification were shown as habitat on field maps.

### Survey Methodology

Because the motivation for our study was to locate timberline sparrows, we focused our survey efforts on predicted areas and did not systematically survey nonpredicted areas. This approach precluded accurate estimation of omission errors, but allowed us to survey a large proportion of predicted sites.

We defined a survey site as a large, relatively continuous area of predicted pixels (Figure 3). Given the inherent difficulties of access in wilderness areas, we did not conduct surveys randomly, and eliminated from consideration sites that were inaccessible due to terrain or private property concerns. In June and July 1999, we surveyed 40 predicted sites. While hiking to predicted sites, we also identified and surveyed 10 sites that were not predicted by the GIS map but that appeared to have suitable timberline sparrow habitat.

We first visually inspected each predicted site to see if the vegetation structure roughly matched our definition of suitable habitat. This definition included: 1) deciduous or coniferous krummholz vegetation < 5 m high arranged in patches; or 2) stunted conifers with dense branching at the base. We played back male timberline sparrow songs to increase our detections of territorial males at all sites. Males often respond aggressively to song playback on their territory by approaching the speaker, perching within view, counter-singing, or all three. Females are not known to sing, but sometimes also approach recordings. We broadcast songs at approximately 100 m intervals throughout each survey site. At each point, we played four songs at moderate volume, followed by another four to six songs at higher volume. When we found timberline sparrows, we obtained a minimum count of territorial males in the area and recorded breeding activity (e.g., active nests, adults carrying food or nesting material, courtship feeding), the composition and structure of the plant community, and other birds seen or heard in the area.

Of the 20 predicted sites with unsuitable habitat, we surveyed 10 using recordings to confirm that timberline sparrows were absent from areas we considered unsuitable habitat. The remaining 10 predicted sites with unsuitable habitat, while clearly visible from below or across a valley, would have been very difficult to access on foot and therefore were not surveyed with playback. The 10 apparently suitable but unpredicted sites that we identified were surveyed with playback.

## Results

Classification of the original dataset yielded mixed results. Ninety-five percent of the 60 locations where timberline sparrows had been present fell within areas predicted to be habitat, and 79% of the 194 locations where birds had not been detected correctly fell within areas not predicted to be habitat by the GIS model. However, only 36.4% of the total area predicted to be timberline sparrow habitat had ≥50% probability of correct classification. In all, 1072 $km^2$ had ≥50% probability of containing suitable habitat, amounting to 4.6% of the study area.

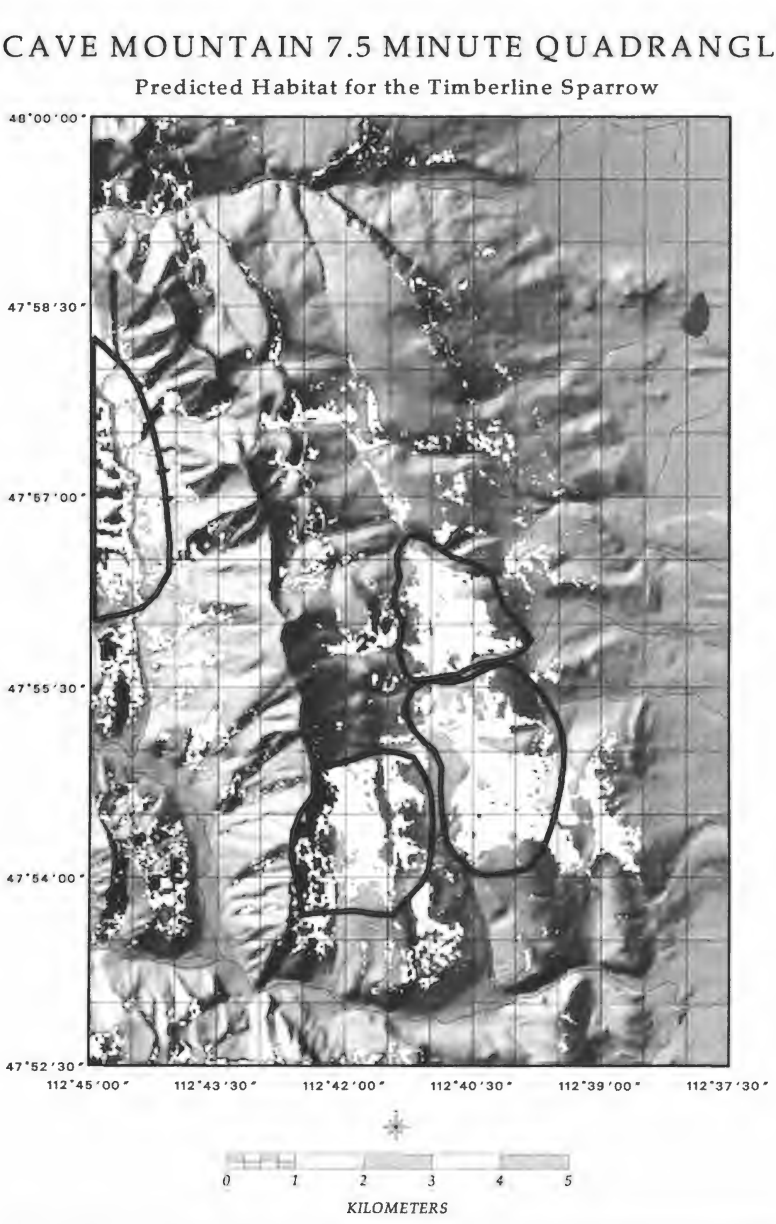


Figure 3. Field map for Cave Mountain 7.5 minute quadrangle, showing predicted habitat with ≥50% likelihood of correct classification in relation to topographic relief. The four survey sites are outlined.

Of the 40 predicted sites inspected within the LCNF, 20 (50%) appeared to have suitable habitat. Of the 20 sites with suitable habitat, we found timberline sparrows at four sites (Table 2). These four sites represent 20% of the predicted sites that matched our definition of suitable habitat, but only 10% of all predicted sites inspected. Timberline sparrows were absent at all 10 survey sites that

TABLE 2. Summary of survey efforts for timberline sparrows for sites that were/were not predicted by the GIS model.

| | Number Assessed | Number with suitable habitat | Number with timberline sparrows |
|---|---|---|---|
| Predicted | 40 | 20 | 4 |
| Not predicted | many[1] | 10 | 1 |

[1]Additional areas were assessed visually for suitable habitat while hiking to predicted sites. Those that had apparently suitable habitat were surveyed.

were predicted by the model but lacked suitable habitat. Of the 10 sites not predicted by the model, but that appeared to have suitable habitat, we found birds at one, Swift Reservoir (Table 3), which was below the elevation cutoff for the model.

The majority of the predicted sites lacking suitable habitat supported scattered, tall conifers (> 5 m), with the remainder of sites supporting grass, common juniper (*Juniperus communis*), or forb communities. It is impossible to assign percentages to sites with specific types of unsuitable habitat because, at many sites, combinations of cover types were found.

Timberline sparrows were found in three different habitat types (Table 3): in krummholz subalpine fir high on an east-facing slope at Mt. Baldy; in stunted subalpine fir and Douglas-fir *(Pseudotsuga menziesii)* in valley bottoms at Jones Creek, Crazy Creek, and Sheep Creek; and in low-growing deciduous shrubs on the shore of Swift Reservoir. The elevation of these sites ranged from ~1450 m at Swift Reservoir to ~2030 m on Mt. Baldy. Timberline sparrows were associated with a variety of tree and shrub species, including subalpine fir, Douglas-fir, quaking aspen *(Populus tremuloides)*, alder *(Alnus* spp.*)*, shrubby cinquefoil *(Pentaphylloides floribunda)*, whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), lodgepole pine *(P. contorta)*, huckleberry (*Vaccinium* spp.*)*, and willow.

We found one active nest containing four eggs at Jones Creek (Figure 2). It was 40 cm above the ground in a ~1m tall Douglas-fir. This discovery extends the known breeding range of the timberline sparrow 50 km south and 41 km east. In this region, the species most often found with timberline sparrows were white-crowned sparrows (*Zonotrichia leucophrys*) and chipping sparrows (*Spizella passerina*). Mountain bluebirds (*Sialia currucoides*), dark-eyed juncos (*Junco hyemalis*), Townsend's solitaires (*Myadestes townsendi*), American robins (*Turdus migratorius*), and MacGillivray's warblers (*Oporornis tolmiei*) were also commonly seen or heard in areas occupied by timberline sparrows. At Swift Reservoir, a clay-colored sparrow (*Spizella pallida*) and a timberline sparrow were singing from the same tree.

## Discussion

Our discovery of five previously unknown populations of timberline sparrows and the extension of this subspecies' known breeding range in northwestern Montana attest to the utility of GIS models for basic ecological research. Despite limited time and data, we were able to generate a map of potentially suitable habitat, which allowed us to focus our survey efforts on sites where we were

TABLE 3. Summary of survey results at sites where timberline sparrows were found.

| Site | USGS Quad | Predicted by GIS | Dominant vegetation | Number of birds | Breeding status |
|---|---|---|---|---|---|
| Mt. Baldy | Hyde Creek | Yes | Krummholz subalpine fir | 8 | Unknown |
| Swift Reservoir | Swift Reservoir | No | Mixed deciduous shrubs | 2 | Unknown |
| Sheep Creek | Walling Reef | Yes | Willow and krummholz subalpine fir | 3 | Unknown |
| Crazy Creek | Gateway Pass | Yes | Subalpine fir | 4 | Probable (male singing long songs) |
| Jones Creek | Cave Mountain | Yes | Douglas-fir | 13 | Confirmed (nest with eggs) |

most likely to find timberline sparrows. Moreover, we found little indication that the model systematically failed to predict suitable habitat (errors of omission). Conversely, model design and issues inherent in mapping the range of a little-known species can explain high rates of over-prediction (errors of commission).

## Model Performance

We calculated a commission error rate of 50% for habitat and 90% for birds. However, we feel the model performed reasonably well. For several reasons, calculations of error rates and statistical tests of model fit are inappropriate for this study (Karl et al. 2000). First, a large number of locations are required to assess model accuracy across an extensive area; over several thousand $km^2$, we found only 30 locations that fit our definition of suitable habitat in the field and only five locations with timberline sparrows. Second, model accuracy must be estimated within the range of the species; the southern part of our study region may have been outside the breeding range of the timberline sparrow. Third, rates of commission error are based on both true absence and apparent absence; the latter is inversely related to sampling effort. Our surveys took place in a single year, and, in most cases, we visited sites only once for a few hours. Thus, our detection rate for birds may have been less than 100%, although using similar methods, we detected birds in virtually all suitable habitat in Glacier NP (Walker 2000).

We expected the model to have a fairly high commission rate because we classified as predicted all pixels with a ≥50% probability of containing suitable habitat. When building a GIS model to predict habitat or species occurrence, commission error rate must be balanced with omission error rate, because a rise in one usually corresponds with a reduction in the other (Karl et al. 2000). Because our primary objective was to locate an uncommon species, for which the factors driving distribution are not well understood, we chose to accept a high commission error rate to minimize omission errors. Although we did not conduct systematic surveys of unpredicted sites, the model appeared to have the desired low omission error rate; we hiked almost 1000 km in the study area and found only 10 unpredicted sites with suitable habitat and only one unpredicted site with timberline sparrows. Our emphasis on avoiding omission error and the failure of our sampling design to determine the exact rates of such error would be inappropriate if management decisions were to be based on the model, but for our purposes, our methods were the most expedient.

Weaknesses inherent in our GIS model may have increased the error rate. The initial data used to build the model were sparse and may have contained some inaccuracies because they were collected by triangulation by hand with a compass, rather than with a global positioning system unit. A larger and more accurate set of initial presence-absence data, systematically collected across the entire landscape, would likely have improved model accuracy. However, in this and other situations, initial models must often be built with limited datasets and periodically improved as more data become available. The structure of treeline habitats also presents some problems for GIS modeling. Patches of krummholz used by timberline sparrows are often smaller than the 30 x 30 m pixel size for the GIS data we used to build the model (Walker 2000), which hinders the classification of presence data and obscures differences between presence and absence classes. Errors may also stem from extrapolating model results beyond the range of the original data. We assumed that we could use spectral class and elevation to identify patchy krummholz – common at treeline in Glacier NP – in the LCNF, a region with different climate and geology. Instead we found that mid-aged subalpine woodlands apparently have a reflectance pattern similar to timberline sparrow habitat. It may be impossible to eliminate this source of error from the model unless vegetation structure can be directly correlated with precipitation or another factor that can be readily mapped in a GIS.

## Distribution, Abundance, and Breeding Status

We have shown that the breeding range of the timberline sparrow extends south of Glacier NP into the LCNF. The relatively high abundance of birds at several sites suggests that we did not simply find a few stray individuals; rather, these sites appear to be regularly occupied habitat. On the other hand, the absence of these birds from many sites with apparently suitable habitat indicates that their distribution may be controlled by factors that we have not modeled, such as interspecific competition (Reed 1982, Robinson and Terborgh 1995), variation in vegetation composition or architecture

(Parrish 1995), conspecific attraction (Stamps 1987, Muller et al. 1997), or geographical variation in habitat preferences (Collins 1983).

### Management Implications

Efforts to discover the distribution of the timberline sparrow should be continued. Although this subspecies is not currently threatened by habitat loss, global climate change (Weisberg and Baker 1995, Hessl and Baker 1997) and the widespread decline of whitebark pine due to introduced pathogens (Keane et al. 1994, Kendall and Keane 2001) may significantly alter the structure and composition of treeline habitats in the Rocky Mountains. Baseline information on distribution and abundance will allow future management decisions to be based on sound information. We have demonstrated that, even with limited data, the use of a GIS model may be an inexpensive and effective way to develop and test working habitat models that locate uncommon species such as the timberline sparrow.

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## Literature Cited

American Ornithologists' Union. 1998. Checklist of North American birds. 7th ed. American Ornithologists' Union, Washington, D. C.

Andries, A. M., H. Gulinck, and M. Herremans. 1994. Spatial modeling of the barn owl, *Tyto alba*, habitat using landscape characteristics derived from SPOT data. Ecography 17:278-287.

Aspinall, R., and N. Veitch. 1993. Habitat mapping from satellite imagery and wildlife survey data using a Bayesian modeling procedure in a GIS. Photogrammetric Engineering and Remote Sensing 59:537-543.

Bolstad, P. V., and T. M. Lillesand. 1992. Improved classification of forest vegetation in northern Wisconsin through a rule-based combination of soils, terrain, and Landsat Thematic Mapper data. Forest Science 38:5-20.

Collins, S. L. 1983. Geographic variation in habitat structure of the black-throated green warbler *(Dendroica virens)*. Auk 100:382-389.

Doyle, T. J. 1997. The timberline sparrow, *Spizella (breweri) taverneri*, in Alaska, with notes on breeding habitat and vocalizations. Western Birds 28:1-12.

ESRI 1998. ArcInfo version 7.1.1. Environmental Systems Research Institute, Inc., Redlands, California.

Frank, T. D. 1988. Mapping dominant vegetation communities in the Colorado Rocky Mountain Front Range with Landsat Thematic Mapper and digital terrain data. Photogrammetric Engineering and Remote Sensing 54:1727-1734.

Grinnell, J., D. Dixon, and J. Linsdale. 1930. Natural history of the vertebrates of the Lassen Peak region of northeast California. University of California Publications in Zoology 35:425-427.

Grinnell, J. 1932. An United States record of the timberline sparrow. Condor 34:231-232.

Griscom, L. 1928. *Spizella taverneri* on migration in Montana. Auk 45:509-510.

Hepinstall, J. A., and S. A. Sader. 1997. Using Bayesian statistics, Thematic Mapper satellite imagery, and breeding bird survey data to model bird species probability of occurrence in Maine. Photogrammetric Engineering and Remote Sensing 63:1231-1237.

Hessl, A. E., and W. L. Baker. 1997. Spruce-fir growth changes in the forest-tundra ecotones of Rocky Mountain National Park, Colorado, USA. Ecography 20:356-367.

Horler, D. N., and F. J. Ahern. 1986. Forestry information content of Thematic Mapper data. International Journal of Remote Sensing 7:405-428.

Karl, J. W., P. J. Heglund, E. O. Garton, J. M. Scott, N. M. Wright, and R. L. Hutto. 2000. Sensitivity of species habitat-relationship model performance to factors of scale. Ecological Applications 10:1690-1705.

Keane, R. E., P. Morgan, and J. P. Menakis. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. Northwest Science 68:213-229.

Kendall, K. C., and R. E. Keane. 2001. Whitebark pine decline: infection, mortality, and population trends. Pages 221-242 *In* D. F. Tomback, S. F. Arno, and R. E. Keane (editors), Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, D. C.

Klicka, J., R. M. Zink, J. C. Barlow, W. B. McGillivray, and T. J. Doyle. 1999. Evidence supporting the recent origin and species status of the timberline sparrow. Condor 101:577-588.

Klicka, J., R. M. Zink, J. C. Barlow, W. B. McGillivray, and T. J. Doyle. 2001. The taxonomic rank of *Spizella taverneri*: a response to Mayr and Johnson. Condor 103:420-422.

Lloyd, A. H. and L. J. Graumlich. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. Ecology 78:1999-1210.

Mayr, E., and N. K. Johnson. 2001. Is *Spizella taverneri* a species or subspecies? Condor 103:418-419.

McTaggart-Cowan, I. 1946. Notes on the distribution of *Spizella breweri taverneri.* Condor 48:93-94.

Muller, K. L., J. A. Stamps, V. V. Krishnan, and N. H. Willits. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds *(Troglodytes aedon).* American Naturalist 150:650-661.

Parrish, J. D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813-1820.

Peteet, D. 2000. Sensitivity and rapidity of vegetational response to abrupt climate change. Proceedings of the National Academy of Sciences 97:1359-1361.

Reed, T. M. 1982. Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: playback and removal experiments. Animal Behavior 30:171-181.

Rimmer, C. C., J. L. Atwood, K. P. McFarland, and L. R. Nagy. 1996. Population density, vocal behavior, and recommended survey methods for Bicknell's thrush. Wilson Bulletin 108:639-649.

Robinson, S. K., and J. Terborgh. 1995. Interspecific aggression and habitat selection by Amazonian birds. Journal of Animal Ecology 64:1-11.

Rotenberry, J. T., M. A. Patten, and K. L. Preston. 1999. Brewer's sparrow *(Spizella breweri).* Pages 1-24 *In* A. Poole and F. Gill (editors), The Birds of North America, No. 390. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Skidmore, A. K. 1998. Nonparametric classifier for GIS data applied to kangaroo distribution mapping. Photogrammetric Engineering and Remote Sensing 64:217-226.

Stamps, J. A. 1987. Conspecific attraction and aggregation in territorial species. American Naturalist 1:329-347.

Steele, B. M., J. C. Winne, and R. L. Redmond. 1998. Estimation and mapping of misclassification probabilities for thematic land cover maps. Remote Sensing of Environment 66:192-202.

Swarth, H. S. 1926. Birds and mammals of the Atlin region of southeast Alaska. University of California Publications in Zoology 30:130-131.

Walker, B. L. 1999. The distribution, abundance, and breeding status of Timberline Sparrows (*Spizella [breweri] taverneri*) in Glacier National Park in 1998. Unpublished report on file at Glacier National Park, West Glacier, Montana.

Walker, B. L. 2000. The distribution, abundance, and breeding status of Timberline Sparrows (*Spizella [breweri] taverneri*) in Glacier National Park, 1998-1999. Unpublished report on file at Glacier National Park, West Glacier, Montana.

Weisberg, P. J., and W. L. Baker. 1995. Spatial variation in tree regeneration in the forest-tundra ecotones, Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 25:1326-1329.

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# Use of Conifer Stumps in Clearcuts by Bats and Other Vertebrates

## Abstract

Although conifer stumps can constitute a large proportion of the volume of wood remaining in clearcuts, the amount and pattern of use of conifer stumps by bats and other vertebrates is poorly known. We made 18,168 observations of conifer stumps in four clearcuts to examine use of bark crevices on conifer stumps in clearcuts in western Oregon. Use of bark crevices by vertebrates did not exceed 1.5% of the stumps searched during any survey with upper 95% confidence intervals not exceeding 5%. Ten species of vertebrates were observed using bark crevices, with the western fence lizard most often detected. Use of stumps by bats was primarily limited to long-eared myotis. Most stumps used by vertebrates were relatively large Douglas-fir stumps located in open areas. Although bark crevices on conifer stumps in clearcuts provide habitat for some species of vertebrates they do not provide the breadth or long-term value as habitat for bats and other vertebrates as snags. Management of roost structures for bats, including the long-eared myotis, should focus on maintaining present and future availability of snags in an area.

## Introduction

Dead wood is widely recognized as an important habitat component for wildlife and provides foraging, nesting, and roosting habitat for many species of amphibians, birds, mammals, and reptiles (Harmon et al. 1986, Maser et al. 1988, Bull et al. 1997, McComb and Lindenmayer 1999). Cavity-nesting birds and forest-dwelling bats are the two primary groups of species that depend extensively on snags (Bull et al. 1997, McComb and Lindenmayer 1999, Hayes 2003) and populations of some cavity-nesting birds are reduced if snags are not present or removed from an area (Mannan et al.1980, Zarnowitz and Manuwal 1985, Schreiber and deCalesta 1992, Sholwalter and Whitmore 2002). Although it is likely that abundance of many species of forest-dwelling bats are similarly linked to snag abundance, response of populations of forest-dwelling bats to removal of snags in coniferous forests has not been demonstrated empirically.

The removal of snags and decadent trees during forest management using standard logging, safety, and site establishment methods reduces the abundance of snags in a stand (Harmon et al. 1986, Spies and Cline 1988) and limits the availability of roosts for bats. As a consequence of the removal of dead wood during logging, conifer stumps often constitute a significant proportion of the wood remaining in a stand (Rolstad et al. 1998). Although some species of amphibians, cavity-nesting birds, forest carnivores, reptiles, and small mammals use highly decayed stumps in forested habitats (Steventon and Major 1982, Morrison et al. 1983, Spencer 1987, Bull and Holthausen 1993, Butts and McComb 2000, McCay 2000), use of conifer stumps with relatively little decay in young clearcuts has rarely been documented and our understanding of the importance of conifer stumps in young clearcuts as potential habitat for bats and other vertebrates that use snags is limited (Vonhof and Barclay 1997).

Vonhof and Barclay (1997) first documented use of bark crevices on conifer stumps in young clearcuts by non-reproductive male and female long-eared myotis (*Myotis evotis*) using visual searches (15 roosts in 14 stumps). Using radio telemetry, Waldien et al. (2000) found that reproductive female long-eared myotis often used conifer stumps, especially in areas primarily managed for timber production with little older forest. These data, combined with no evidence of use of stumps from telemetry work on other species of forest-dwelling bats (Campbell et al. 1996; Vonhof

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and Barclay 1996, 1997; Brigham et al. 1997; Ormsbee and McComb 1998; Waldien et al. 2000), suggest that conifer stumps offer regular roosting opportunities only for long-eared myotis, especially in intensively managed areas with limited numbers of snags. If stumps provide regular roosting habitat for long-eared myotis, then long-eared myotis should be frequently observed using stumps given their use of stumps (Vonhof and Barclay 1997, Waldien et al. 2000) and the availability of stumps in intensively managed areas. However, our understanding of the importance of conifer stumps as potential roosts to all species of forest-dwelling bats and the extent and pattern of use of stumps by the long-eared myotis remains limited.

Our objectives were to document the extent of the use of bark crevices on conifer stumps by bats and other vertebrates (amphibians and reptiles) in clearcuts harvested 6-10 yr earlier and to determine if amount of use changed during the summer. Furthermore, we were interested in determining if characteristics of stumps were associated with use by vertebrates that could be expected to use bark crevices on conifer stumps in this region.

## Methods

We conducted the study on the west slope of the Cascade Mountains in Lane County, Oregon, between 44°30' and 43°58' north latitude and 123°50' and 122°30' west longitude. Climate in the study area is mild with average minimum temperatures of -2 to -5°C in January and average maximum temperatures of 24 to 29°C in July (Franklin and Dyrness 1988). Study sites were within the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1988).

The study area encompasses three major drainage systems: Fall Creek, Little Fall Creek, and South McKenzie River (Waldien 1998). Douglas-fir (*Pseudotsuga menziesii*) was the dominant overstory species in these areas; western hemlock and western redcedar (*Thuja plicata*) were minor components in many stands. Clearcuts were generally replanted with Douglas-fir after harvest. The Fall Creek watershed had relatively little timber harvest and is generally characterized by large blocks of forests >80 yr old. The Little Fall Creek watershed and the South McKenzie River area are primarily under private ownership and have been managed for high timber yield; these areas are generally dominated by younger forests (<80 yr) with a few small areas of older forests remaining.

We identified all clearcuts in Little Fall Creek watershed and the South McKenzie River area that were 6-10 yr old and were located within 2.4 km of open water. Clearcuts with these characteristics are typical of those used by long-eared myotis in the study area (Waldien et al. 2000). We randomly selected four stands (Booth Kelly, Coopers, Wader, and Little Fall) from the population of available stands; Coopers stand was known to have been used in 1996 by female long-eared myotis. Selected stands were ≥4.0 km apart. The Booth Kelly stand (22.9 ha, 670 saplings/ha), was harvested in 1989, was located on an easterly aspect, and was ca. 1.5 km from a pond. Forest stands in the immediate vicinity generally were closed canopy forests <80 yr old with some younger clearcuts interspersed. The Coopers (easterly aspect, 32.8 ha, 1640 saplings/ha) and Wader (northerly aspect, 46.5 ha, 885 saplings/ha) stands were located within 0.2 km of ponds and were harvested in 1989 and 1988. Forest stands in the immediate vicinity of both stands were generally younger clearcuts; there was an area of older, closed canopy forests >80 yr old downslope from the Wader stand. The Little Fall stand (21.0 ha, 820 saplings/ha) was harvested in 1988, was located on relatively level terrain with a slight westerly aspect, and was immediately adjacent to Little Fall Creek. Forest stands in the immediate vicinity generally were closed canopy forests <80 yr old with some younger clearcuts interspersed.

We paired stands for sampling based on physical proximity and road access for logistical reasons. We surveyed one pair of stands every other week between 7 May and 18 August 1997. Surveys at each pair of stands generally were completed on the same day except for surveys prior to 10 June and one survey during the week of 14 August when only one stand was surveyed in a day. Prior to 10 June, we searched 200-400 stumps per stand per day. Starting 10 June, we surveyed 600 stumps per stand and two stands per day, except on 14 August when we searched all stumps in the Little Fall stand.

For surveys conducted between 10 June and 18 August, we divided each stand into three areas of equal size and randomly identified two start-

ing points in each area. We examined the first 100 conifer stumps with top diameters ≥10 cm encountered within a 6 m wide belt transect oriented along a randomly selected compass bearing from the starting point. A new direction was selected if a transect intercepted the edge of the stand. Individual stumps could be resampled during different surveys.

We visually located vertebrates in bark crevices on stumps by carefully pulling exfoliating bark away from the wood and visually inspecting the crevice (Vonhof and Barclay 1997). Flashlights, mirrors, and probes were used occasionally to inspect crevices. A probe was used to move bats to the opening of the crevice where they were carefully removed by hand. We attempted to extract only one bat from a roost for species identification to limit disturbance to the roost when more than one bat was observed within a crevice, and we assumed that bats remaining in the roost were of the same species. On several occasions, more than one bat was captured as it attempted to exit the roost. These observations supported our assumption that only one species simultaneously occupied individual roosts. Bats were identified to species and we determined their sex, age (Anthony 1988), and reproductive status (Racey 1988). Bats were individually marked with a tattoo punch (Boncorrosa and Smythe 1972) to allow identification of individuals in subsequent searches. All other vertebrates were extracted only if necessary for species identification. We did not attempt to distinguish among species of garter snakes (*Thamnophis* sp.). Although we occasionally observed western fence lizards (*Sceloporus occidentalis*), northern alligator lizards (*Elgaria coeruleus*), and garter snakes basking on stumps, these observations were not recorded because our objectives focused on use of bark crevices and because of potential sampling biases resulting from basking animals frequently fleeing upon our approach.

Although it is possible vertebrates were missed during searches of bark crevices, our estimate is a realistic estimate because <50% of the stumps sampled had any crevice that a vertebrate could enter and the vast majority of stumps with crevices were structurally simple with small crevices that were easily searched. Few stumps had large or complex bark crevices that would interfere with our ability to successfully detect individuals in a crevice.

We measured six habitat variables at all stumps used by vertebrates and at a subset of randomly selected stumps. During surveys prior to 10 June, we collected habitat data for all stumps searched. Starting 10 June, we randomly selected five of the six transects in a survey and measured habitat data on the first and last 10 stumps in each of the five transects (100 stumps) one time each month in each stand to increase the number of stumps searched in a stand during each visit. Each stump was identified to species and was classified as having or lacking a crevice under exfoliating bark with a minimum opening of 10 x 3 cm and a depth ≥10 cm (adapted from Waldien et al. 2000). We visually estimated the percentage of bark remaining on the stump (<5%, 5 to 40%, 41 to 75%, or >75%) and percent cover of vegetation or dead wood within 5 m that limited a bat from accessing the stump (≤50%, 51-75%, or 76-100%). We classified the height on the tallest side (0-25 cm, 26-100 cm, 101-200 cm, or >200 cm) and diameter (average of 2 perpendicular measures; 10-40 cm, 41-70 cm, 71-100 cm, or >100 cm) of each stump.

We used numerical methods (Leemis and Trivedi 1996) to construct exact 95% confidence intervals for the binomial proportion of stumps used on each sampling occasion. We tested the hypothesis that species used stumps independently of measured habitat characteristics using Fisher's exact test (Ramsey and Schafer 1997). However, since we found significant differences in all six characteristics of stumps among the four stands (Chi-square tests, all $P$-values <0.0001), we conducted tests on a stand-by-stand basis and restricted our analyses to used and available stumps that had crevices, and to species of vertebrates with ≥12 observations. Based on these criteria, we only tested for associations between stump use and habitat characteristics for the western fence lizard in one stand, and for the northern alligator lizard in two stands.

We made additional observations of vertebrates in conifer stumps in other stands in our study area during a contemporaneous study of long-eared myotis (Waldien et al. 2000). These observations are not included in analyses of extent of use or associations with characteristics of stumps, but are presented to provide a more complete documentation of use of bark crevices by bats and other vertebrates.

## Results

We made 18,168 observations of conifer stumps during 32 systematic searches in four clearcuts (8 searches per stand; Table 1). We identified six species of vertebrates in bark crevices on 79 conifer stumps (81 observations) and detected four additional species during ancillary searches of conifer stumps in other stands (Table 1). Frequently a single species accounted for the majority of observations in a stand and no species was observed using stumps in all four stands (Table 1). Western fence lizards and northern alligator lizards were the most commonly observed species. Long-eared myotis was the only species of bat encountered during systematic surveys (7 roosts in 6 stumps) and was the species most often observed during ancillary searches in other stands (Table 1). California myotis (*Myotis californicus*), fringed myotis (*M. thysanodes*), and Yuma myotis (*M. yumanensis*) were observed infrequently using stumps during ancillary searches in other stands (Table 1). All were solitary adult males.

Estimated use of stumps by vertebrates (all species combined) ranged from 0 (95% CI = 0.0-0.6%) to 1.5% (95% CI = 0.5-4.3%) of the stumps searched (n = 0-20 stumps) during a given survey (Figure 1). Observations of vertebrates in bark crevices suggest seasonal shifts in use. Bats and reptiles were observed most often from June to September prior to the onset of fall rains, and clouded salamanders (*Aneides ferreus*) were observed most often after the onset of fall rains in September. Amphibians represented only 3.4% of the vertebrates observed in bark crevices from May through August (n = 88 vertebrates), but represented a much higher proportion of observations in September (n = 20 vertebrates; 30%) and October (n = 14 vertebrates; 64%). Conversely, bats and reptiles represented 96.4% of observations from May through August and relative observations of bats and reptiles decreased in September (70%) and October (36%).

We observed bats roosting in stumps on 24 occasions (systematic and ancillary searches combined). The majority of the roosts comprised single bats (17 of 24 roosts); four roosts had 2 bats each and each of three additional roosts had 4, 5, and 14 bats. The largest colony of bats (14 bats) we observed was in a high cut stump. Of the 24 bats extracted from roosts, we identified 12 adult (9 females, 3 males) and 8 juvenile (6 females, 2 males) long-eared myotis. We observed juvenile long-eared myotis roosting singly in stumps on four separate occasions.

TABLE 1. Observations of vertebrates in bark crevices during systematic surveys of conifer stumps in four stands in western Oregon, during May to August, 1997, and ancillary searches for vertebrates in conifer stumps, during July 1996 to September, 1997.

| | Systematic Searches | | | | | |
|---|---|---|---|---|---|---|
| | Stands | | | | | |
| | Booth Kelly | Coopers | Wader | Little Fall | Total | Ancillary Searches |
| Stumps Searched | 3,900 | 4,200 | 4,350 | 5,718 | 18,168 | |
| Species | | | | | | |
| California myotis | 0 | 0 | 0 | 0 | 0 | 2 |
| Long-eared myotis | 0 | 2[a] | 1 | 4[b] | 7[a,b] | 13 |
| Fringed myotis | 0 | 0 | 0 | 0 | 0 | 1 |
| Yuma myotis | 0 | 0 | 0 | 0 | 0 | 1 |
| Clouded salamander | 0 | 2 | 1 | 0 | 3 | 17 |
| Pacific tree frog | 0 | 0 | 0 | 0 | 0 | 1 |
| Northern alligator lizard | 12 | 9 | 0 | 1 | 22 | 5 |
| Western skink | 0 | 0 | 0 | 1[c] | 1[c] | 0 |
| Western fence lizard | 0 | 2 | 3 | 39[c] | 44[c] | 5 |
| Garter snake | 2 | 1 | 1 | 0 | 4 | 0 |
| Total | 14 | 16[a] | 6 | 44[b,c] | 81[a,b,c] | 45 |

[a] one stump was a maternity roost of 14 bats.

[b] one stump was used on two different occasions by adult females and another stump was a maternity roost of two adult females.

[c] one stump was used simultaneously by a western skink and a western fence lizard in two separate crevices.

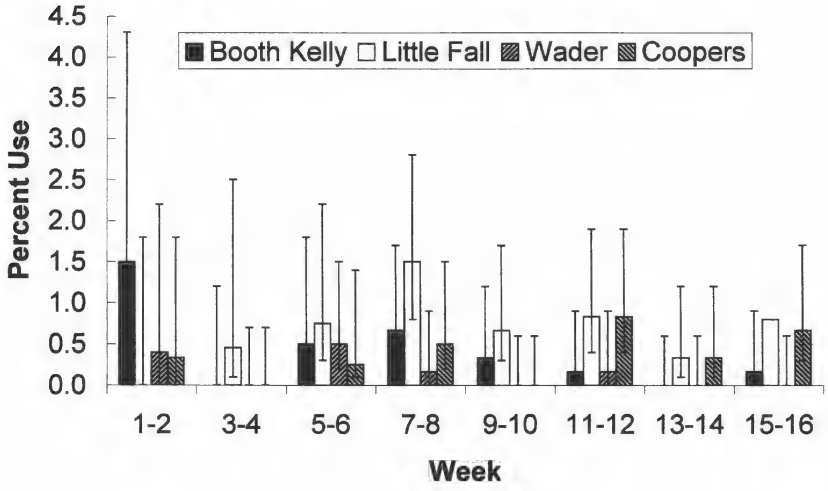


Figure 1. Patterns of detection of vertebrates in bark crevices on conifer stumps during systematic surveys in four stands in western Oregon, during May to August, 1997. The final survey in the Little Fall stand represents an inventory of stumps.

Although we did not systematically monitor individual stumps for repeated use, we did observe use of one stump on two occasions by different female long-eared myotis. We also observed stumps previously used as roosts by female long-eared myotis (Waldien et al. 2000) being used by other bats or other species of vertebrates on nine occasions (two clouded salamanders, one western fence lizard, one Yuma myotis, and five long-eared myotis). Two of the stumps used repeatedly by long-eared myotis contained at least one adult female in reproductive condition, two contained solitary juveniles, and one contained an adult male long-eared myotis. Based on distinct punch-marks given to bats when they were originally captured night-roosting together, one juvenile may have been offspring of the female long-eared myotis previously tracked to the stump using telemetry.

Forty-seven percent of the stumps searched had bark crevices with a minimum opening of 10 x 3 cm and a depth ≥10 cm. The general pattern of observations of vertebrates in stumps reflected the availability of stumps, with most observations in Douglas-fir stumps 26-100 cm tall, 10-70 cm in diameter, and with ≤75% cover (Table 2). We found evidence that northern alligator lizards were associated with stump height, bark remaining, and cover but the pattern was inconsistent between the two stands. In the Coopers stand, alligator lizards were associated with taller stumps ($P = 0.002$) and stumps with low levels of cover ($P = 0.01$), but stump height ($P = 0.50$) and cover ($P = 0.20$) did not appear to influence their use in the Booth Kelly stand. In both the Booth Kelly and Coopers stands, alligator lizards were detected more frequently than expected in stumps with 5-40% bark and less frequently than expected in stumps with 41-75% bark (Booth Kelly $P = 0.06$, Coopers $P = 0.02$). In Booth Kelly, alligator lizards were also detected more frequently than expected in stumps with >75% bark (Booth Kelly $P = 0.06$). Height, diameter, and cover were related to use of stumps by western fence lizards, which were most frequently detected using taller stumps ($P = 0.004$) and stumps with little cover ($P < 0.0001$). Western fence lizards were detected more frequently than expected in stumps with a diameter of 10-40 cm and less than expected in stumps with a diameter of 71-100 cm ($P = 0.03$).

## Discussion

Conifer stumps likely provide limited habitat for some species of forest-dwelling bats in clearcut forest stands in western Oregon. Our data demonstrate that a small proportion of the available stumps are used for roosting at any given time, and the vast majority are likely never used, despite

TABLE 2. Habitat characteristics of 2229 random stumps and 79 stumps used by vertebrates during systematics searches in 4 clearcuts in western Oregon, summer 1997. One observation of a western skink is not included.

| Variable | Random | Long-eared Myotis | Clouded salamander | Northern alligator lizard | Western fence lizard | Garter snake | All Species |
|---|---|---|---|---|---|---|---|
| Crevice | | | | | | | |
| Present | 981 | 6 | 3 | 22 | 44 | 4 | 79 |
| Not Present | 1248 | 0 | 0 | 0 | 0 | 0 | 0 |
| Species | | | | | | | |
| Douglas-fir | 1747 | 4 | 3 | 14 | 37 | 3 | 61 |
| Western Hemlock | 446 | 1 | 0 | 8 | 5 | 1 | 16 |
| Western Redcedar | 36 | 1 | 0 | 0 | 2 | 0 | 2 |
| Bark (%) | | | | | | | |
| <5% | 142 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5-40% | 326 | 0 | 2 | 9 | 10 | 0 | 21 |
| 41-75% | 662 | 4 | 0 | 2 | 14 | 1 | 21 |
| >75% | 1099 | 2 | 1 | 11 | 20 | 3 | 37 |
| Diameter | | | | | | | |
| 10-40 cm | 1175 | 3 | 2 | 7 | 23 | 0 | 35 |
| 41-70 cm | 873 | 2 | 0 | 11 | 19 | 1 | 33 |
| 71-100 cm | 133 | 1 | 1 | 3 | 1 | 2 | 8 |
| >100 cm | 48 | 0 | 0 | 1 | 1 | 1 | 3 |
| Height | | | | | | | |
| 0-25 cm | 69 | 1 | 0 | 1 | 4 | 0 | 6 |
| 26-100 cm | 1837 | 4 | 2 | 11 | 33 | 2 | 52 |
| 101-200 cm | 277 | 0 | 1 | 7 | 7 | 2 | 17 |
| >200 cm | 46 | 1 | 0 | 3 | 0 | 0 | 4 |
| Cover | | | | | | | |
| ≤50% | 383 | 4 | 0 | 9 | 27 | 1 | 41 |
| 51-75% | 478 | 2 | 1 | 7 | 10 | 3 | 23 |
| 76-100% | 1368 | 0 | 2 | 6 | 7 | 0 | 15 |

the large number of stumps potentially available in an area following harvest. In addition, our observations are consistent with previous work suggesting that only the long-eared myotis uses stumps on a semi-regular basis (Vonhof and Barclay 1997, Waldien et al. 2000). Observations of little brown myotis (*Myotis lucifugus*) (Kalcounis and Hecker 1996), Yuma myotis (Table 1; Vonhof and Barclay 1997), southwestern myotis (*M. auriculus*) (Bernardos 2001), fringed myotis (Table 1), and California myotis (Table 1) roosting in stumps appear to represent infrequent occurrences. Although female long-eared myotis regularly roost in stumps in areas with limited snags (Waldien et al. 2000), relatively few female long-eared myotis or other bats are captured at sites with low densities of snags within 2.5 km of the capture site (E. B. Arnett, Oregon State University, Corvallis, unpublished data). This is consistent with the hypothesis that limited snag resources in an area may limit populations of forest-dwelling bats, even long-eared myotis that is known to roost in stumps.

Use of bark crevices on conifer stumps by vertebrates is likely influenced by weather and varies seasonally among species. Use by bats and reptiles is greatest during warm and dry periods when stumps in open areas offer higher temperatures (Vonhof and Barclay 1997). Wet and cool conditions that likely occur in bark crevices on stumps during spring and fall rains in western Oregon are likely to be unfavorable for bats and reptiles because they would negatively impact their ability to thermoregulate effectively. Conversely, use of bark crevices by clouded salamanders was greatest during the fall and use of bark crevices by amphibians may be largely restricted to cool and moist periods. These data suggest that habitat value and patterns of use of stumps varies seasonally, and that seasonal influences vary among taxa.

Use of bark crevices on stumps in clearcuts appears to be further limited by the phenology of bark exfoliation and decay of stumps, and by the timing of plant succession and stand development in the clearcut. Previous research demonstrated

that use of stumps by bats is largely restricted to a period of a few years between the time crevices form and surrounding vegetation covers the stump (Waldien et al. 2000). Similarly, we observed that western fence lizards were associated with tall stumps with little vegetative cover. This observation is consistent with previous observations of western fence lizards using stumps for basking and foraging (Adolph 1990, Chase 1998). Stumps in areas with little vegetative cover experience higher temperatures (Vonhof and Barclay 1997) and may offer sites where fence lizards and other species can thermoregulate effectively (Lillywhite and North 1974). Thus, it appears that use of stumps by reptiles is also strongly influenced by development of the surrounding vegetation, and that use by reptiles is greatest during the first few years following timber harvest. In contrast, crevices in stumps likely offer habitat for amphibians until crevices are filled with debris or the bark fully exfoliates. Increasingly cool and moist microclimatic conditions in a stand as overstory development proceeds are likely to create increasingly favorable conditions for amphibians through time.

Our observations of 10 species of vertebrates in bark crevices in conifer stumps, in conjunction with observations that several species of cavity-nesting birds have been observed to use stumps (Morrison et al. 1983), suggest that stumps do provide some habitat for vertebrates in clearcuts, particularly when other sources of dead wood are scarce or lacking (Rolstad et al. 1998, Waldien et al. 2000). However, we contend that stumps only provide a fraction of the habitat value of large snags because of the limited time period they are available for use. Further, although several species of bats and other vertebrates can use stumps (Vonhof and Barclay 1997, Rolstad et al. 1998, Waldien et al. 2000), most species select for larger snags (Morrison et al. 1983) and many more species of vertebrates use snags than those that can use stumps. Large, moderately decayed, conifer snags are the primary roost structures for long-eared myotis and other forest-dwelling bats (Campbell et al. 1996, Vonhof and Barclay 1996, Brigham et al. 1997, Ormsbee and McComb 1998, Waldien et al. 2000, Weller and Zabel 2001, Hayes 2003) and management of roosting habitat for bats, including the long-eared myotis, should focus on maintaining present and future availability of snags.

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## Literature Cited

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315-327.

Anthony, E. L. P. 1988. Age determination in bats. Pages 47-58 *In* T. H. Kunz (editor), Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, D. C.

Bernardos, D. A. 2001. Use of ponderosa pine-Gamble oak forests by bats in northern Arizona. M.S. Thesis, Northern Arizona University, Flagstaff, Arizona.

Bonaccorso, F. J., and N. Smythe. 1972. Punch-marking bats: an alternative to banding. Journal of Mammalogy 53:389-390.

Brigham, R. M., M. J. Vonhof, R. M. R. Barclay, and J. C. Gwilliam. 1997. Roosting behavior and roost site preferences of forest-dwelling California bats (*Myotis californicus*). Journal of Mammalogy 78:1231-1239.

Bull, E. L., and R. S. Holthausen, 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. Journal of Wildlife Management 57:335-345.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs important to wildlife in the interior Columbia River Basin. USDA Forest Service General Technical Report PNW-GTR-391. Pacific Northwest Research Station, Portland, Oregon.

Butts, S. R., and W. C. McComb. 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. Journal of Wildlife Management 64:95-104.

Campbell, L. A., J. G. Hallet, and M. A. O'Connell. 1996. Conservation of bats in managed forests: Use of roosts by *Lasionycteris noctivagans*. Journal of Mammalogy 77:976-984.

Chase, J. M. 1998. Central-place forager effects on food web dynamics and spatial pattern in northern California meadows. Ecology 79:1236-1245.

Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-306.

Hayes, J. P. 2003. Habitat ecology and conservation of bats in western coniferous forests. *In* C. J. Zabel and R. G. Anthony (editors), Mammal community dynamics in coniferous forests of western North America: management and conservation. Cambridge University Press, Cambridge, United Kingdom *(in press)*.

Kalcounis, M. C., and K. R. Hecker. 1996. Intraspecific variation in roost-site selection by little brown bats (*Myotis lucifugus*). Pages 81-90 *In* R. M. R. Barclay and R. M. Brigham (editors), Bats and Forests Symposium, October 19-21, 1995, Victoria, British Columbia, British Columbia Ministry of Forests Research Program, Working Paper 23/1996, Victoria, British Columbia.

Leemis, L. M., and K. S. Trivedi. 1996. A comparison of approximate interval estimators for the Bernoulli parameter. The American Statistician 50:63-68.

Lillywhite, H. B., and F. North. 1974. Perching behavior of *Sceloporus occidentalis* in recently burned chaparral. Copeia 1:256-257.

Mannan, R. W., E. C. Meslow, and H. M. Wight. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:787-797.

Maser, C., R. F. Tarrent, J. M. Trappe, and J. F. Franklin, Technical Editors. 1988. From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland, Oregon.

McCay, T. S. 2000. Use of woody debris in cotton mice (*Peromyscus gossypinus*) in a southeastern pine forest. Journal of Mammalogy 81:527-535.

McComb, W., and D. Lindenmayer. 1999. Dying, dead, and down trees. Pages 335-372 *In* M. L. Hunter, Jr. (editor), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, United Kingdom.

Morrison, M. L., M. G. Raphael, and R. C. Heald. 1983. The use of high-cut stumps by cavity-nesting birds. Pages 73-79 *In* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels (technical coordinators), Snag Habitat Management: Proceedings of the Symposium. USDA Forest Service General Technical Report, RM-99. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Ormsbee, P. C., and W. C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. Journal of Wildlife Management 62:596-603.

Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-46 *In* T. H. Kunz (editor), Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, D. C.

Ramsey, F. L., and D. W. Schafer. 1997. The Statistical Sleuth: A Course in Methods of Data Analysis. Duxbury Press, Belmont, California.

Rolstad, J., P. Majewski, and E. Rolstad. 1998. Black woodpecker use of habitats and feeding substrates in a managed Scandinavian forest. Journal of Wildlife Management 62:11-23.

Schreiber, B., and D. S. deCalesta. 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. Forest Ecology and Management 50:299-316.

Sholwalter, C. R., and R. C. Whitmore. 2002. The effect of gypsy moth defoliation on cavity-nesting bird communities. Forest Science 48:273-281.

Spencer, W. D. 1987. Seasonal rest-site preferences of pine martens in the northern Sierra Nevada. Journal of Wildlife Management 51:616-621.

Spies, T. A., and S. P. Cline. 1988. Coarse woody debris in forests and plantations of coastal Oregon. Pages 5-24 *In* C. Maser, R. F. Tarrent, J. M. Trappe, and J. F. Franklin (technical editors), From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland, Oregon.

Steventon, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. Journal of Wildlife Management 46:175-182.

Vonhof, M. J., and R. M. R. Barclay. 1996. Roost site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Canadian Journal of Zoology 74:1797-1805.

Vonhof, M. J., and R. M. R. Barclay. 1997. Use of tree stumps as roosts by the western long-eared bat. Journal of Wildlife Management 61:674-684.

Waldien, D. L. 1998. Characteristics and spatial relationships of day-roosts and activity areas of female long-eared myotis (*Myotis evotis*) in western Oregon. M.S. Thesis, Oregon State University, Corvallis, Oregon.

Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared myotis in western Oregon. Journal of Wildlife Management 64:785-796.

Weller, T. J, and C. J. Zabel. 2001. Characteristics of fringed myotis day roosts in northern California. Journal of Wildlife Management 65:489-497.

Zarnowitz, J. E., and D. A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management 49:255-263.

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# Spatial Use and Habitat Associations of Columbian White-tailed Deer Fawns in Southwestern Oregon

## Abstract

Fawns represent a critical life history stage in the dynamics of deer populations, yet little recent information is available on the ecology of neonatal Columbian white-tailed deer (CWTD), a geographically isolated and federally endangered sub-species. We described home ranges, areas of concentrated use, and habitat associations of CWTD fawns in southwestern Oregon during the summers of 1997 and 1998. Spatial use patterns and habitat use within areas of concentrated use were described for 11 radio-marked fawns. Pooled habitat use was described for 24 radio-marked fawns. Areas of concentrated use averaged 2.4 ha, which was 13.3% of mean 95% home range size (18.0 ha). Frequent use of oak-madrone woodland and riparian cover types characterized fawn habitat use patterns. Cover types containing conifers were rarely used and usually not available within home ranges. Although we found no detectable patterns of habitat selection or avoidance among fawns, areas of concentrated use were composed mostly of oak-madrone woodland (35%) and riparian (26%) cover types. Moreover, 74% of concentrated use area was within 200 m of streams. Our results provide useful information on habitat characteristics used frequently by CWTD fawns.

## Introduction

Columbian white-tailed deer (*Odocoileus virginianus leucurus*; CWTD) are a sub-species that was once ubiquitous throughout western Oregon and Washington, but now exists as two geographically isolated and federally endangered sub-populations (Smith, 1985a). The Douglas County sub-population of CWTD in southwestern Oregon was listed as endangered in 1967, but has been proposed recently for delisting (U.S. Fish and Wildlife Service 2002).

Although much research on spatial use and habitat associations has been conducted on fawns in other white-tailed deer populations (McCullough 1979, Porath 1980, Ozoga and Verme 1986, Huegel et al. 1986), little recent information exists on the life history characteristics of CWTD neonates. Smith (1982) conducted an extensive study of CWTD ecology approximately 20 yr ago and described habitat use for 45 marked CWTD fawns within the Douglas County sub-population. He concluded that CWTD were strongly associated with riparian areas, oak woodland, and shrub dominated habitats, and that habitat selection by fawns was related primarily to thermoregulation followed by adequacy of escape/hiding cover. Furthermore, he suggested that the extirpation of CWTD from much of its historic range was linked to the reduction of lowland riparian and oak woodland habitats. Inferences on neonatal movement patterns were limited, however, because radio telemetry techniques were not widely used during all years of his study.

The neonatal period represents a critical life stage in deer population dynamics, and the characteristics of this life stage need elucidation (Jackson et al. 1972). Estimates of spatial use such as home range and core areas are useful in determining the areal requirements of a species (Bingham and Noon 1997), and act as surrogates for resource distribution for post-partum females, abundance of fawn hiding cover, or fawn predation risk (Mace and Harvey 1983, Ozoga and Verme 1986). Habitat associations of neonatal deer (and maternal females) are complicated because they are influenced to various degrees by several factors including predation risk, climate exposure, and

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forage availability (Main and Coblentz 1996, Bowyer et al. 1998).

An understanding of macrohabitat associations of CWTD fawns is important to identify the habitat features that characterize fawning and rearing areas. Because CWTD are an endangered species, managers must make informed decisions regarding habitats that may be critical for fawns and postpartum females. Section 3 of the Endangered Species Act 1973 defines critical habitat, in part, as areas within the geographical range of species that contain physical and biological attributes essential to the conservation of a species and which may require special management considerations and protection. From a biological perspective, however, critical habitat is directly associated with an animal's fitness and can only be determined from manipulative studies (White and Garrott 1990). Unfortunately, these manipulative studies are rarely practical, but composition of habitat attributes within areas that receive disproportionate use may give managers useful information for habitat conservation planning (Samuel et al. 1985, Bingham and Noon 1997).

Our objective was to determine spatial use and habitat associations for CWTD fawns in the Douglas County sub-population. We simply described the magnitude and variation of fawn spatial use patterns. Our research questions regarding habitat associations were 1) how variable are patterns of habitat use and selection among fawns? 2) can variation in habitat use be explained by fawn gender, diel period, and fawn age? and 3) what habitat attributes characterize areas of concentrated use?

## Study Area

We monitored CWTD within the lower North Umpqua River watershed in Douglas County, Oregon. The study area was bordered approximately by the towns of Roseburg to the south, Glide to the east, and Sutherlin to the north. Interstate 5 formed the western boundary. Elevation ranged from 165 to 595 m. Rainy winters and hot dry summers characterized the climate. Monthly average temperatures during our study ranged from 5.4°C in December to 21.1°C in August. Average annual precipitation was 108.1 cm, and ranged monthly from 0.5 cm in July to 24.3 cm in December (Western Region Climate Center, Reno, Nevada). Snowfall was rare.

Smith (1982, 1985b) provided an extensive description of plant communities and species composition in the study area. Whereas some stands of continuous deciduous hardwood/mixed-conifer forest and undisturbed riparian areas were present, vegetation communities most often represented a relatively disturbed environment due to past or current history of fire management, grazing, agricultural conversion, and housing development. Essentially, a mosaic of finely interspersed Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), madrone (*Arbutus menziesii*), and grassland plant associations intersected by numerous riparian drainages characterized the study area. Large expanses of coniferous forest were rare, and smaller conifer stands normally were logged previously and regenerating. Rural housing or residential development bordered or intersected many parts of the study area.

## Methods

Fawns were captured by hand between late May and early July 1997-1998. Three capture techniques were employed: 1) drives along transects, 2) observing behaviors exhibited by females, and 3) opportunistic encounters. We attempted to search all cover types to obtain random samples of marked fawns. Captured fawns were fitted with expandable breakaway radio-collars equipped with mortality sensors. We estimated ages of fawns by measuring hoof growth (Haugen and Speake 1958) and degree of umbilicus scabbing. Fawns were not weighed because we wanted to minimize overhandling that may result in abandonment (Livezey 1990).

We located fawns three to five times per week during diurnal, crepuscular, and nocturnal periods. We tracked fawns in a systematic random fashion to ensure that all fawns would be located at different times. We relied heavily on obtaining visual or estimated visual (i.e., homing in) locations to avoid problems associated with radio telemetry error. When triangulations were necessary (n = 23), we were usually within 200 m of the signal and used a bearing standard deviation of 5.78° to construct error ellipses. Successive locations of individual fawns were at least 12 hr apart to maintain temporal independence (White and Garrott 1990). We located fawns as early as 0400 to as late as 2300 PST to ensure adequate

representation of diurnal and nocturnal movements (Beyer and Haufler 1994). A location was recorded as biased and discarded if a fawn fled the area because of observer presence and we were unable to determine its location before it fled. Triangulated locations whose error ellipse exceeded the size of the cover type containing the location were also discarded. Cover type, location type (visual, estimated visual, or triangulation), and diel period were also recorded. Diel periods were defined as crepuscular (2 hr before and after sunrise or sunset), diurnal (2 hr after sunrise to 2 hr before sunset), and nocturnal (2 hr after sunset to 2 hr before sunrise). We plotted all locations in the field on 1:24000 USGS topographic maps. Although we continued to locate and monitor fawns that remained alive for the life of the radio-collar, only locations obtained between the date of capture and mid-September (i.e. summer months) were used for spatial use and habitat association analyses. This resulted in a scope of inference to approximately the first three to four months of life.

Cover types and streams were delineated from scanned 7.5 minute ortho-photo quadrangle maps. Minimum cover type patch size was 1-ha. Cover types listed in Table 1 were categorized based upon a modification of detailed descriptions of percent coverage and species composition (Smith 1982,1985b). Streams were buffered to produce 5–100 m distance to stream classes (≤ 100 m, 101–200 m, 201–300 m, 301–400 m, > 400 m).

## Spatial Use

We calculated estimates of spatial use for 11 fawns with greater than 20 locations each. Fixed kernel density estimators with bandwidths calculated using least squares cross validation (Seaman and Powell 1996) were used to estimate 99% and 95% utilization distributions, or home ranges, with the

TABLE 1. Description of cover types used to analyze habitat associations of Columbian white-tailed deer fawns in southwestern Oregon, summer 1997-1998.

| Cover Type | Canopy cover | Typical plant species and general characteristics |
|---|---|---|
| Grassland | Shrub: < 25%<br>Tree: < 5 % | Tall fescue (*Lolium arundinaceum*), perennial ryegrass (*Lolium perenne*), dogstail (*Cynosurus echinatus*), subterranean clover (*Trifolium subterraneum*). Included grazed pastures and prescribed fire was occasionally applied. |
| Grass shrub | Shrub: > 25%<br>Tree: < 5% | Poison oak (*Toxicodendron diversilobum*), wild rose (*Rosa* sp.), hawthorne (*Crataegus* sp.), blackberry (*Rubus* sp.). Also included clear-cuts. |
| Oak-madrone savanna | Shrub: <5%<br>Tree: > 5 and < 50% | Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), madrone (*Arbutus menziesii*). |
| Oak-madrone savanna shrub | Shrub: > 25%<br>Tree: > 5 and < 50% | Same species as oak-madrone savanna and grass shrub. |
| Oak-madrone woodland | Shrub: variable<br>Tree: > 50% | Same as oak-madrone savanna. Oaks were more common on mesic sites, whereas madrone was more common on xeric sites. Understories were characterized by poison oak and wild rose. |
| Oak-madrone conifer | Shrub: variable<br>Tree: > 50% | Same as oak-madrone woodland, plus Douglas-fir (*Pseudotsuga menziesii*) and western red cedar (*Thuja plicata*). Conifer canopy cover > 25 and < 90%. Understories are usually poorly developed. |
| Conifer | Shrub: variable<br>Tree > 50% | Conifer canopy cover > 90%. Usually monotypic Douglas-fir stands with poorly developed understories. |
| Riparian | Shrub: variable<br>Tree: variable | Oregon ash (*Fraxinus latifolia*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), Oregon white oak, common rush (*Juncus effusus*), sedge (*Carex* sp.). Narrow strips generally consisting of areas between 10 and 50 m of a stream. |
| Yard | Shrub: variable<br>Tree: variable | Areas within 50 m of human development. Houses, gardens, lawns, small orchards and tree farms. |

program KERNELHR (Seamen et al. 1998). Areas of concentrated use were estimated using the KERNELHR subroutine PLOTCNTR (Seaman et al. 1998). PLOTCNTR estimates an area of concentrated use by calculating the average observation density of all locations in a given set and then determines the contour where the observation density is greater than average. The average observation density is calculated as the sum of the linear array of the observed densities divided by the number of observed locations. This methodology avoids subjective and arbitrary contour selections, and each area of concentrated use is based solely on the density of locations for an individual fawn. We refrained from calling areas of concentrated use core areas because they were not tested against a null distribution of bivariate uniform locations within the home range (Samuel et al. 1985, Bingham and Noon 1997). Differences by sex were not tested because of the small sample size of fawns with spatial use estimates; therefore only descriptive statistics are reported.

### Habitat Associations

We determined cover type use by pooling all fawn locations. We could not measure habitat use for individual fawns because of the relatively small mean number of locations per fawn ($20 \pm 6$), which would have resulted in insufficient power to detect individual habitat use patterns (White and Garrott 1986). A chi-square test was used to determine if frequency of use was equal among all cover types. Differences in cover type use by sex, diel period, and neonatal/post-neonatal period were tested with chi-square contingency tables. The neonatal period was the date of capture through 15 July (ca. 45 days for most fawns), and the post-neonatal period was 15 July through 1 September. These natal periods served as a surrogate for fawn age, and 15 July was chosen as the cutoff date because we assumed most fawns had been borne and alive for at least 1 mo (see results). Conifer cover types were never used and were deleted from chi-square analyses. We calculated the precision of cover type use estimates with 95% confidence intervals for proportions (Ramsey and Schafer 1997).

We tested for selection of cover types and distance to stream classes within fawn home ranges (i.e., third-order selection) (Johnson 1980). Use of cover types and distance to stream classes within areas of concentrated use was estimated by first pooling areas of concentrated use and then calculating the mean percent composition by area of cover types and distance to stream classes. Availability was defined as the mean percent composition by area of cover types and distance to stream classes within 99% fixed kernel home ranges. Variance for use and availability estimates was calculated with 95% confidence intervals for proportions. We tested for selection of cover types and distance to stream by comparing 95% confidence intervals for areas of concentrated use (used areas) to 99% fixed kernel home ranges (available areas). Selection was inferred if confidence limits for availability did not overlap estimates of mean use. This selection analysis used the individual marked animal as the sample unit. Sample sizes were the number of fawn home ranges containing a particular cover type or distance to steam class. We pooled 1–11 fawns to estimate mean percent composition of a cover types, and 5 - 9 fawns for distance to stream classes, because not all cover types or distance to stream classes were available to fawns within their home range.

## Results

We captured and radio collared 24 fawns: 16 (5 males, 11 females) in 1997, and 8 (5 males, 3 females) in 1998. The mean date of capture was 15 June (SE = 1.4 days), although fawns continued to be captured through 3 July. Mean age at capture was $5.7 \pm 0.7$ days for 20 fawns that could be aged accurately. After removing locations with observer bias and excessive telemetry error, we obtained a total of 413 locations from 11 fawns to describe spatial use and habitat selection, and 469 locations from all fawns to describe habitat use.

### Spatial Use

Based on an average of 38 locations per fawn, mean 95% and 99% home range size was $18.0 \pm 4.8$ ha and $24.3 \pm 6.9$ ha. Mean area of concentrated use size was $2.4 \pm 0.7$ ha. On average, areas of concentrated use were found near the $71 \pm 1.5$% contour of observed location densities, and encompassed an area that included only $13.3 \pm 0.9$% of the 95% utilization distribution area (Table 2). Variability in spatial use among fawns was evident as coefficients of variation for spatial use estimates were relatively high (CV 95% home range = 94%, CV 99% home range = 88%, CV area of concentrated use = 94%).

TABLE 2. Individual estimates and descriptive statistics for 99% and 95% fixed kernel home ranges and areas of concentrated use for 11 Columbian white-tailed deer fawns in southwestern Oregon, summer 1997-1998.

| Deer ID | Sex | No. locations | 99% home range area (ha) | 95% home range area (ha) | Concentrated use area (ha) | Concentrated use area contour (%) | Concentrated use : 95% home range area (%) |
|---|---|---|---|---|---|---|---|
| 1130 | female | 30 | 19.5 | 14.9 | 1.2 | 69.6 | 7.9 |
| 1150 | female | 31 | 9.1 | 7.0 | 0.7 | 67.1 | 9.6 |
| 1750 | female | 44 | 29.7 | 22.9 | 3.6 | 78.9 | 15.7 |
| 1820 | female | 57 | 11.6 | 7.8 | 1.1 | 69.5 | 14.6 |
| 1890 | female | 43 | 41.4 | 30.0 | 3.6 | 61.8 | 11.9 |
| 1140 | male | 30 | 17.0 | 11.7 | 1.8 | 76.2 | 15.4 |
| 1240 | male | 25 | 11.6 | 8.7 | 1.4 | 74.6 | 15.7 |
| 1260 | male | 41 | 14.5 | 15.1 | 1.5 | 66.4 | 9.7 |
| 1790 | male | 54 | 86.3 | 60.4 | 8.5 | 68.6 | 14.1 |
| 1830 | male | 27 | 6.3 | 4.7 | 0.7 | 74.6 | 15.4 |
| 1860 | male | 31 | 19.9 | 15.1 | 2.4 | 73.4 | 15.8 |
| mean | | 38 | 24.3 | 18.0 | 2.4 | 71.0 | 13.3 |
| SE | | 3 | 6.9 | 4.8 | 0.7 | 1.5 | 0.9 |
| range | | 25 – 57 | 6.3 - 86.3 | 4.7 - 60.4 | 0.7 - 8.5 | 61.8 - 78.9 | 7.9 - 15.8 |

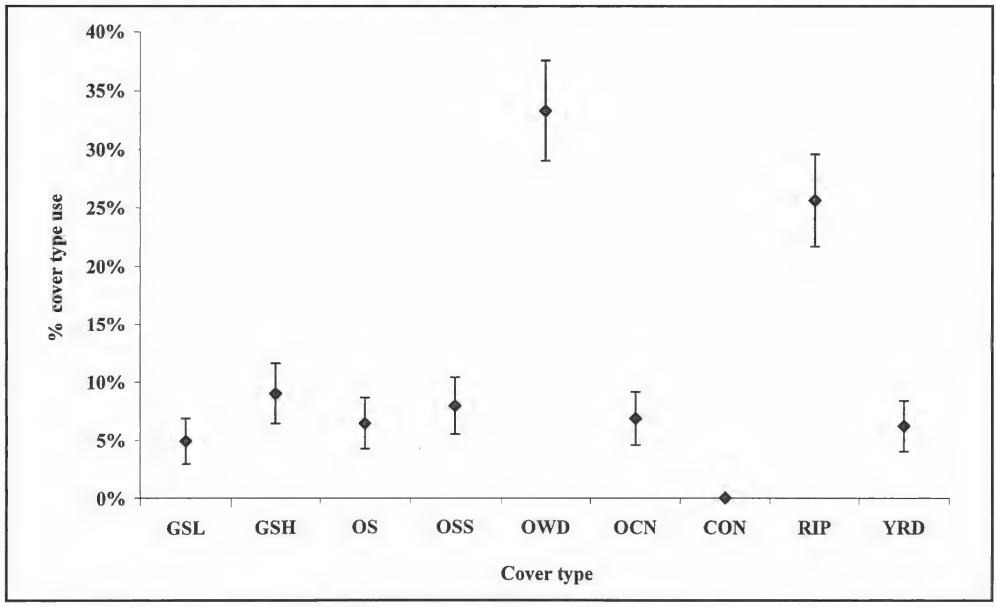


Figure 1. Mean percentage (and 95% confidence intervals) of Columbian white-tailed deer fawn locations (n = 469) by cover type in southwestern Oregon, summer 1997-1998. GSL = grassland, GSH = grass shrub, OS = oak-madrone savanna, OSS = oak-madrone savanna shrub, OWD = oak-madrone woodland, OCN = oak-madrone conifer, CON = conifer, RIP = riparian, YRD = yard.

## Habitat Associations

Frequency of use differed among cover types when all fawn locations were pooled ($\chi^2 = 308.7$, $P < 0.0001$). Oak-madrone woodland was the most frequently used cover type (33%) followed by riparian (26%). All other cover types were used < 10% of the time except conifer, which was never used (Figure 1). Cover type use varied by sex ($\chi^2 = 82.1$, $P < 0.0001$). Female use of grass-shrub was 17% compared to no use by males. Conversely,

males used oak-madrone woodland (42%) and yards (12%) more frequently than females (25% and 1%). Cover type use varied by diel period with sexes pooled ($\chi^2 = 17.83$, $P = 0.01$). Higher use of riparian areas occurred during crepuscular/nocturnal periods (34%) compared to diurnal periods (21%), while slightly higher use of yards occurred during diurnal periods (8%) compared to crepuscular nocturnal periods (3%). Cover type use did not differ significantly between neonatal and post neonatal periods with sexes pooled.

Oak-madrone woodland (35%) and riparian (26%) cover types constituted the largest average percentage of areas of concentrated use. Less than 10% of average concentrated use areas comprised other cover types. Conifer cover types were absent from all areas of concentrated use and composed < 3% of home range area (Figure 2). Areas of concentrated use were near streams, as 52% and 74% of their cumulative area was within 100 m and 200 m of a stream. Less than 20% of average concentrated use areas comprised distance to stream classes > 201 m (Figure 2). However, use and availability were variable among individual fawns. Thus, selection for particular cover types and distance to stream classes was not detected because confidence limits for availability within 99% home ranges overlapped estimates of mean use in areas of concentrated use for all cover types and distance to stream classes (Figure 2).

## Discussion

### Spatial Use

Ostensibly, the relatively small home ranges and areas of concentrated use of CWTD fawns in this study reflected their sedentary nature during the early stages of life (Jackson et al. 1972). Furthermore, only a small percentage of fawn home ranges were used most of the time because areas of concentrated use were 13% of home range size but contained 71% of all locations (Table 2). Relatively similar spatial use patterns were observed among CWTD adult females (Ricca 2000). It is also noteworthy that the average area contour delineating areas of concentrated use in this study was 71%, which is substantially greater than the 50% contour that is often arbitrarily chosen to delineate core areas. These results suggest that core areas should be determined quantitatively from observed distributions of animal locations instead of arbitrary delineations.

Variability in spatial use estimates among fawns in this study was similar to estimates reported for other white-tailed deer in Texas (Carroll and Brown 1977) and Michigan (Ozoga and Verme 1986), and mule deer (*Odocoileus hemionus*) in Montana (Riley and Dood 1984) and Washington (Steigers and Flinders 1980). Home range and movements of neonates are largely maternally controlled and variation could be attributed to maternal age (Ozoga and Verme 1986). Spatial use estimates also reflect resource distribution (Mace and Harvey 1983). Accordingly, variation in fawn home range size may have represented different availability of hiding cover for fawns or high quality forage for lactating maternal females, which resulted in different movement patterns among individuals.

### Habitat Associations

Fawns in this study used primarily oak-madrone woodland and riparian cover types (Figure 1). These observed patterns of cover type use corroborate those estimated by Smith (1982), and were also similar to those exhibited by adult females (Ricca 2000). However, variability in cover type composition within areas of concentrated use and home ranges, suggested a degree of plasticity in fawn/maternal female habitat use, and selection was not evident (Figure 2).

Some variation in habitat use was explained by fawn gender and diel period. For example, male fawns never used grass-shrub but female fawns used it 17% of the time. This higher use of grass-shrub cover types by females supports previous observations of relatively frequent use of this cover type (Smith 1982). Use of riparian areas was also higher during crepuscular-nocturnal periods than diurnal periods in our study. Adult females frequently used open foraging habitat at night (Ricca 2000), so maternal females may have hid their fawns in denser and more secure riparian areas before foraging at night. Fawns should use open cover types more frequently as they mature and begin following their mothers, but we found no differences in habitat use between neonatal and post-neonatal periods. Fawns either continued to follow a hider strategy (Lent 1974) during this time, or maternal females continued to use the same habitats used for parturition.

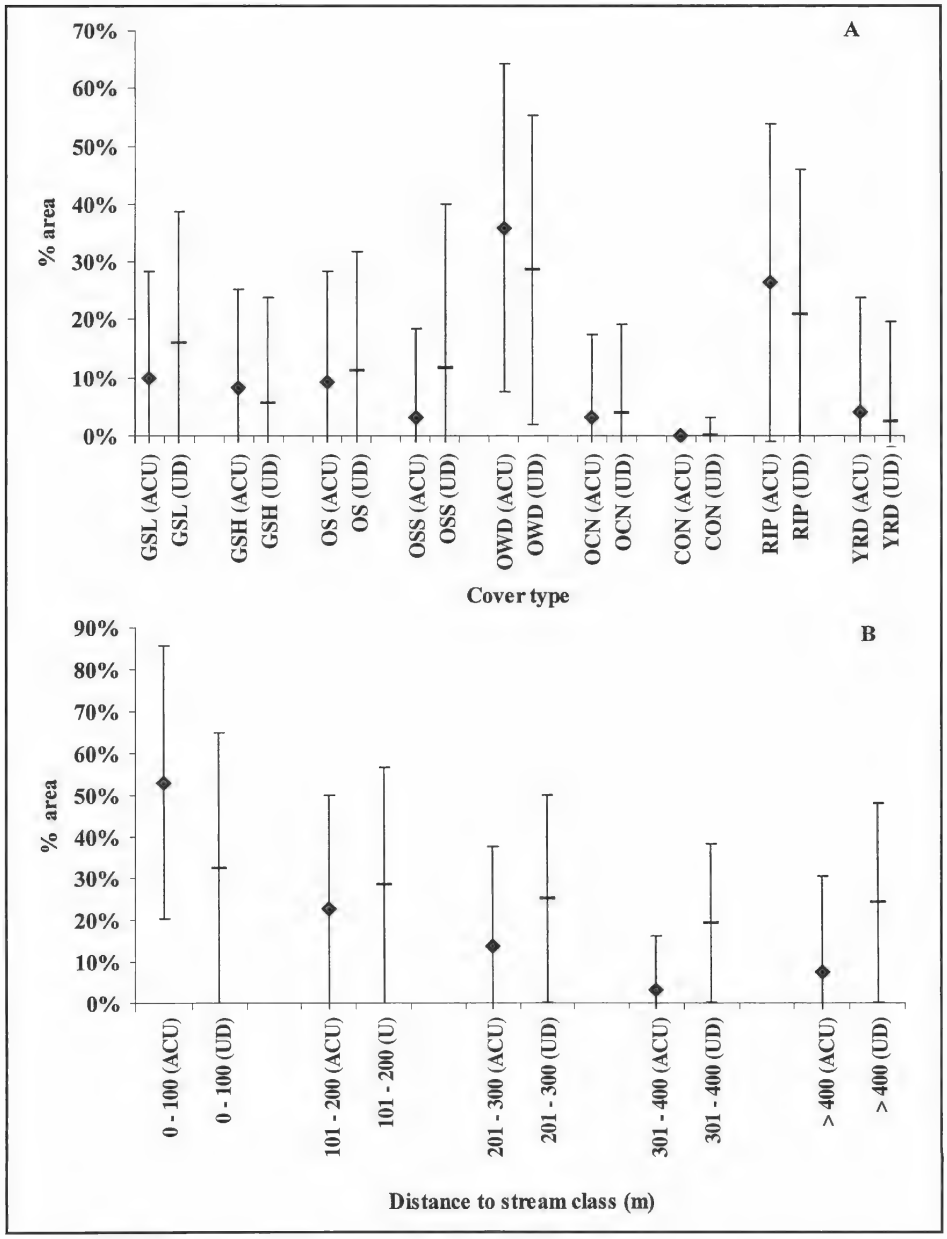


Figure 2. Mean percent composition (and 95% confidence intervals) of cover types (A) and distance to stream classes (B) within pooled areas of concentrated use and 99% fixed kernel utilization distributions for 11 Columbian white-tailed deer fawns in southwestern Oregon, summer 1997-1998. (ACU) = area of concentrated use, (UD) = 99% utilization distribution, GSL = grassland, GSH = grass shrub, OS = oak- madrone savanna, OSS = oak-madrone savanna shrub, OWD = oak-madrone woodland, OCN = oak-madrone conifer, CON = conifer, RIP = riparian, YRD = yard.

Habitat use by fawns and maternal females may represent trade-offs between minimizing predation risk and climatic exposure, against maximizing forage acquisition (Main and Coblentz 1996, Bowyer et al. 1998). June temperatures can exceed 32°C, to which fawns are vulnerable because of their high surface to volume ratio. Thermal cover is defined as vegetative overstories that minimize energetic costs associated with thermoregulation (Demarchi and Bunnell 1993). Although the fitness benefits of thermal cover have been questioned (Hobbs 1989), associations between thermal cover and habitat selection have been inferred in other studies of deer neonates (Fox and Krausman 1994, Bowyer et al. 1998). In this study, the broadleaf overstories of oak-madrone woodlands and riparian areas likely provided neonates relief from excessive heat. In addition, relatively frequent use of riparian areas and habitats < 200 m from streams within areas of concentrated use may indicate greater availability of free water and succulent, high quality vegetation that is important for lactation (Bowyer 1991).

We found no patterns of selection for particular cover types and distance to stream classes (Figure 2), so inferences regarding their relative biological importance are limited. However, our study was designed to examine selection of habitats within home ranges (third-order), yet selection can also occur at higher levels such as selection of a home range (second-order) or geographic range (first-order) (Johnson 1980). Selection is also difficult to detect when resources are ubiquitous within a home range (Johnson 1980). Selection for riparian and oak-madrone cover types may not have been detected because they were relatively common within home ranges. Conversely, low availability of conifer and oak-madrone-conifer within home ranges suggested that these cover types may not have been selected at the home range level. Also, our study lacked sufficient power to detect selection because of the low number of radiocollared fawns (White and Garrott 1986). Thus, lack of selection within home ranges does not necessarily equate with lack of importance. Future studies should evaluate selection of home ranges and the resources they contain across the local range of Douglas County CWTD.

Because such a high frequency of spatial use occurs within a relatively small area, it is plausible to assume that areas of concentrated use for fawns contain resources that contribute to survival and reproductive success of CWTD during this crucial life history stage. Oak-madrone woodlands and habitats within 200 m of streams may represent areas of increased biological importance. Although areas of concentrated use may not provide all necessary resources (Buchanan et al. 1998) and we have no direct measure of fitness, our results will aid managers in determining habitat conservation strategies for this endangered species in a less-arbitrary fashion (Bingham and Noon 1997).

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## Literature Cited

Beyer, D. E. Jr., and J. B. Haufler. 1994. Diurnal versus 24 hour sampling of habitat use. Journal of Wildlife Management 58:178-180.

Bingham, B.C., and B. R. Noon. 1997. Mitigation and habitat "take": application to habitat conservation planning. Conservation Biology 11:127-139.

Bowyer, R. T. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy 72:138-145.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal by black-tailed deer: climate, forage, or risk of predation. Journal of Mammalogy 79:415-425.

Buchanan, J. B., R. J. Fredrickson, and D. E. Seaman. 1998. Mitigation of habitat "take" and the core area concept. Conservation Biology 12:238-240.

Carroll, B. K., and D. L. Brown. 1977. Factors affecting neonatal fawn survival in southern-central Texas. Journal of Wildlife Management 41:36-69.

Demarchi, M. W., and F. L. Bunnell. 1993. Estimating forest canopy effect on summer thermal cover for Cervidae (deer family). Canadian Journal of Zoology 23:2419-2426.

Fox, K. B., and P. R Krausman. 1994. Fawning habitat of desert mule deer. The Southwestern Naturalist 39:269-275.

Haugen, A. O., and D. W. Speake. 1958. Determining age of young white-tailed deer. Journal of Wildlife Management 22:319-321.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101. The Wildlife Society, Incorporated, Bethesda, Maryland.

Huegel, C. N., R. B. Dahlgren, H. L. Gladfelter. 1986. Bedsite selection by white-tailed deer fawns in Iowa. Journal of Wildlife Management 50:474-480.

Jackson, R. M., M. White, and F. F. Knowlton. 1972. Activity patterns of young white-tailed deer fawns in south Texas. Ecology 53:263-270.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Lent, P. C. 1974. Mother infant relationships in ungulates. Pages 14-53 *In* V. Geist and F. Walther (editors), The behavior of ungulates and its relation to management. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Livezey, K. B. 1990. Toward the reduction of marking induced abandonment of newborn ungulates. Wildlife Society Bulletin 18:193-203.

Mace, G. M., and P. H. Harvey. 1983. Energetic constraints on home range size. American Naturalist 121:120-132.

Main, M. B, and B. E. Coblentz. 1996. Sexual segregation in Rocky Mountain mule deer. Journal of Wildlife Management 60:497-507.

McCullough, D. R. 1979. The George Reserve Deer Herd: Population Ecology of a K-selected Species. University of Michigan Press, Ann Arbor, Michigan.

Ozoga, J. J., and L. J. Verme. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. Journal of Wildlife Management 50:480-486.

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Porath, W. R. 1980. Fawn mortality estimates in farmland deer range. Pages 55-63 *In* R. L. Hine and S. Nehls (editors), White-tailed deer population management in the northcentral states. Proceeding of the 1979 North Central Wildlife Society.

Ramsey, F. L., and D. W. Schafer. 1997. The Statistical Sleuth: A Course in Methods of Data Analysis. Duxbury Press, Belmont, California.

Ricca, M. A. 2000. Movements, habitat associations, and survival of Columbian white-tailed deer in western Oregon. M.S. Thesis, Oregon State University, Corvallis, Oregon.

Riley, S. J., and A. R. Dood. 1984. Summer movements, home range, habitat use, and behavior of mule deer fawns. Journal of Wildlife Management 48:1302-1310.

Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711-719.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95-100.

Smith, W. P. 1982. Status and habitat use of Columbian white-tailed deer in Douglas, County, Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Smith, W. P. 1985a. Current geographic distribution and abundance of Columbian white-tailed deer, *Odocoileus virginianus leucurus* (Douglas). Northwest Science 59:243-251.

Smith, W. P. 1985b. Plant associations within the interior valleys of the Umpqua River Basin, Oregon. Journal of Range Management 36:525-530.

Steigers, W. D., and J. T. Flinders. 1980. Mortality and movements of mule deer fawns in Washington. Journal of Wildlife Management 44:381-388.

U.S. Fish and Wildlife Service. 2002. Endangered and threatened plants: supplemental proposed rule to delist the Douglas County population of Columbian white-tailed deer from the federal list of endangered and threatened wildlife. Federal Register 67:42217-42229.

White, G. C., and R. A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. Journal of Wildlife Management 50:509-513.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, California.

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# Characterization of the Floral Odor of Oregongrape: Possible Feeding Attractants for Moths

## Abstract

Moths and other insects at blooms of Oregongrape were sampled with traps during April and May 2001. Moths captured were predominantly the alfalfa looper (43%), and the gooseberry fruitworm (26%) with small numbers of 14 other species in the families Noctuidae and Geometridae. Analyses of samples made from the air around blooms of Oregongrape shrubs revealed the consistent presence of α-pinene, β-pinene, sabinene, E-β-ocimene, β-myrcene, limonene, benzaldehyde, and phenylacetaldehyde. Greatest amounts released per flower per hour were 124.5 ± 40.8 ng phenylacetaldehyde, 87.6 ± 6.7 ng α-pinene, 54.4 ± 17.8 ng E-β-ocimene, and 43.9 ± 7.0 ng limonene. Phenylacetaldehyde and benzaldehyde are known attractants for some moths, including the alfalfa looper. The odor produced by Oregongrape blooms may attract feeding moths for pollination of flowers.

## Introduction

Tall Oregongrape (*Berberis aquifolium*) is endemic to the Pacific Northwest of North America (Peck 1961) and is commonly planted as an ornamental in both residential and commercial settings. The shrub blooms in early spring, producing numerous yellow flowers on an upright raceme. The flowers are odorous to the human nose during the day and at night. Observations of moths, including alfalfa looper moths (*Autographa californica*), flying about strong-smelling blooms of tall Oregongrape in Yakima, Washington, led to this investigation of moth visitors at flowers and the odor of those flowers. We hypothesize that volatile chemicals emitted by flowers of Oregongrape attract these moths to the flowers, where they feed on floral nectar.

Volatile chemicals have been identified from flowers of several plants that are frequented by moths, and some of these chemicals attract moths. Examples of plants that possess flowers attractive to moths are bladderflower (*Araujia sericofera*) (Cantelo and Jacobson 1979), glossy abelia (*Abelia grandiflora)* (Grant 1971, Haynes et al 1991), night-blooming jessamine (*Cestrum nocturnum)* (Heath et al. 1992), Japanese honeysuckle (*Lonicera japonica*) (Pair and Horvat 1997: Schlotzhauer et al. 1996), lesser butterfly orchid (*Platanthera bifolia*) (Plethys 2001), and Drummond's gaura (*Gaura drummondii*) (Teranishi et al. 1991, Lopez et al. 2000). Phenylacetaldehyde from flowers of bladderflower attracts many species of moths (Cantelo and Jacobson 1979). Glossy abelia flowers emit phenylacetaldehyde, benzaldehyde, 2-phenylethanol, and benzyl alcohol, which are attractive to cabbage looper moths: (Haynes et al. 1991). Phenylacetaldehyde, benzyl acetate, and benzyl alcohol, emitted by flowers of night-blooming jessamine, attract cabbage looper moths: (Heath et al. 1992). Cis-jasmone, phenylacetaldehyde, and linalool, which are attractive to several species of moths, are present in extracts of flowers of Japanese honeysuckle (Schlotzhauer et al. 1996, Pair and Horvat 1997). Similarly, five chemicals identified from flowers of Drummond's gaura (phenylacetaldehyde, 2-phenylethanol, limonene, methyl salicylate, and methyl-2-methoxy benzoate) (Teranishi et al. 1991) constitute a blend that attracts corn earworm moths (*Helicoverpa zea)* (Lopez et al. 2000). The gamma moth (*Autographa gamma*) of Eurasia is attracted to lilac aldehydes, methyl benzoate, and benzyl benzoate, which are emitted by flowers of the lesser butterfly orchid *(Platanthera bifolia*) (Plethys 2001).

The alfalfa looper, a close relative of both the gamma moth and the cabbage looper, is a highly polyphagous caterpillar that is a pest of numerous garden and farm crops throughout the western United States. The moth of this species is attracted to some of the same volatile chemicals that are emitted by flowers discussed above. Phenylacetaldehyde and benzyl acetate attract alfalfa looper moths (Landolt et al 2001), cis-jasmone enhances alfalfa looper moth attraction to phenylacetaldehyde, and benzaldehyde enhances

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alfalfa looper moth attraction to benzyl acetate (Landolt et al. 2001). Our general investigation of moth behavior at flowers seeks to understand the roles of different plants as food sources for moths, to understand how moths locate food sources, and to use this information to discover new chemical attractants for management of pest species.

The objectives of this study were to determine what moths might visit flowers of Oregongrape plants, determine if known moth attractants are part of the odor of those flowers, and characterize the floral odor for possible further investigation of these chemicals as insect attractants. We collected and identified moths at flowers of Oregongrape plants, and characterized the volatile chemicals emitted by those flowers. The results support the hypothesis that moth visitation at flowers of this plant is in part a response to floral odor chemistry.

## Methods

Insect visitors to flowers of Oregongrape plants were sampled using large white mesh cone shaped traps (Heliothis traps) placed directly above clusters of open flowers. Insects are trapped when they fly up from flowers into the cone of the trap and cannot escape the upper chamber. Traps were placed over flower clusters in late afternoon (1500 to 1600 hrs P.S.T.) and were checked the following morning (800 to 900 hrs P.S.T.) for insects. We sampled 37 times during April and May 2001: at the Yakima Agricultural Research Laboratory near Wapato (n = 3), Randall Park in the city of Yakima (n = 5), a residence in Yakima (n = 4), Oak Creek Wildlife Preserve (n = 9), Mud Lake (n = 15) west of Yakima, and the Valley Mall in Union Gap (n = 1). All trap sites were in Yakima County, Washington.

Volatiles emitted by flower clusters on Oregongrape shrubs at the USDA-ARS Yakima Agricultural Research Laboratory were collected by a portable volatile collection system, which included an electric air suction pump, flow meter, a gas sampling bag, and a SuperQ trap. Air was pulled through a septum port in the 10 liter Tedlar gas sampling bag housing the flowers, through the flowmeter at a rate of 2-3 L of air per minute, and then through the trap in which odor chemicals were adsorbed. The bag was placed over a branch with flowers and was loosely tied off at the branch stem. Air was pulled through the volatile collection system for 1 hr, during late afternoon or early evening. The volatile collection trap contained 30 mg of SuperQ adsorbent in a 0.635 cm x 6.67 cm long borosilicate glass tube. The trap was extracted with 600 µL of 10% ether in hexane. As a control, similar volatile collections were made over Oregongrape plants that did not possess flowers. The open flowers within volatile collection bags were counted and recorded for computations of chemical amounts emitted per flower per unit time. This volatile collection procedure was followed five times for plants with flowers and nine times for plants without flowers. All collections were made over plants on the grounds of the USDA, ARS, Yakima Agricultural Research Laboratory.

One-microliter aliquots of the extracts of SuperQ traps were analyzed by gas chromatography-mass spectrometry (GC-MS), using a Hewlett Packard 6890 Plus gas chromatograph with a model 5973 electron impact mass selective quadrapole detector. The gas chromatograph was equipped with an HP-1 MS fused silica capillary column (60 m long, 0.25 mm i.d., 25 µm film thickness) and then a DB Wax fused silica capillary column of the same dimensions. Analyses were run at an initial temperature of 40°C for 2 min, increasing 15°C per min to a maximum of 200°C. Mass spectra of eluting peaks were matched to those in the Wiley 275 and NIST98 libraries of compounds to obtain preliminary structural identifications. Structures were confirmed by comparing retention times of eluting peaks with known standards, using both types of GC columns, and by comparing mass spectra of eluting peaks and of known standards to those in the Wiley and NIST data bases.

Additional analyses were conducted to determine the enantiomeric makeup of α- and β-pinene and limonene. Commercial sources of compounds were used as standards that were compared with α-pinene, β-pinene, and limonene from Oregongrape volatile collections. Two samples of Oregongrape odorants (volatile collection trap extract) and standards for (R)- and (S)- α-pinene, (R)- and (S)-β-pinene, and (R)- and (S)-limonene were analyzed on a Hewlett Packard 5890 II Plus GC using a 0.25 mm x 30 m Cyclosil B fused silica capillary column. Temperature program was 40°C for 2 min, increasing 10°C per min to a maximum of 180°C. Kovat's retention indices were

calculated using a homologous series of hydrocarbons to bracket each compound (nonane through dodecane). One extract sample was spiked with the hydrocarbon series before analysis, while another sample was compared to the hydrocarbons in a parallel GC analysis. A sample of racemic α-pinene was also analyzed following the addition of the hydrocarbon series to the sample, for precise determination of retention indices of the two enantiomers and to verify that the two enantiomers were adequately separated using those methods.

Synthetic chemical standards used in establishing GC retention times and for comparing spectroscopic data were purchased from chemical supply companies. These were benzaldehyde, phenylacetaldehyde, β-myrcene, S-(-)-β-pinene, R-(+)-β-pinene, racemic α-pinene, (1R)-(+)-α-pinene, R(+)- and (S-(-)- limonene, sabinene, and (S)-(-)-α-pinene. Synthetic E-β-ocimene was not commercially available. A 93% pure sample of E-β-ocimene was then obtained by HPLC fractionation of pure essential oil of basil which possesses this compound (Özek et al. 1995, Fleisher and Fleisher 1992). The E-β-ocimene was isolated from basil oil using an Agilent 1100 series HPLC equipped with an Agilent Eclipse semiprep column (#XDB-C18, 9.4 mm x 250 mm). A standard flow cell was used with a column-switching valve for collection of fractions from elution with 50% acetonitrile: 50% water at 4 ml/min. Identification of a compound in basil oil as E-β-ocimene was verified by GC-MS analysis under the conditions indicated above.

## Results

Ninety-two moths were captured in traps over Oregongrape flowers, 41 males and 51 females (Table 1). Most moths captured were either alfalfa looper moths (42%), or the gooseberry fruitworm (*Zophodia grossulariella*) (26%). While both male and female alfalfa looper moths were captured, only female and no male gooseberry fruitworm moths were captured in the traps. Eleven other species of noctuid moths and three species of geometrid moths were captured. In addition, 125 honeybees (*Apis mellifera*), 137 queen bumblebees (*Bombus* sp.), 71 other unidentified bees, 23 queen German wasps (*Vespula germanica*), 3 female golden paper wasps (*Polistes aurifer*), and 152 unidentified flies were trapped.

Eight compounds were present in chromatograms from all five air collections made over blossoms of Oregongrape shrubs (Figures 1,2). β-pinene and limonene were present in volatile collections as both enantiomeric forms (Figure 2). These compounds were not detected in samples collected from nonflowering Oregongrape shrubs. The limit of detection was estimated to be about 30 ng per collection, which is a limit of 0.05 ng as a GC peak, and with one µL of the 600 µL sample injected for analysis (0.05 ng/µL x 600 µl/sample = 30 ng/sample).

The largest amounts of chemicals collected were phenylacetaldehyde and S-(-)-α-pinene, followed by E-β-ocimene and limonene (Table 2). The amounts collected were also quite variable, as indicated by the standard errors of the means (Table 2), but the proportions were relatively stable, as is indicated by the smaller standard error values for mean percents of total emissions calculations (Table 2).

TABLE 1. Number of moths captured in traps over clusters of flowers of Oregongrape shrubs. March-May 2001, Yakima County, Washington.

| Species | Males | Females |
|---|---|---|
| Noctuidae | | |
| Plusiinae | | |
| *Autographa californica* | 26 | 13 |
| *Trichoplusia ni* | 1 | 0 |
| Amphipyrinae | | |
| *Apamea cariosa* | 7 | 5 |
| *Apamea cinefacta* | 2 | 1 |
| *Apamea spaldingi* | 1 | 1 |
| Hadeninae | | |
| *Discestra trifolii* | 0 | 2 |
| *Discestra mutata* | 0 | 1 |
| *Discestra oregonica* | 1 | 0 |
| *Dargida procincta* | 1 | 0 |
| *Leucania insueta* | 0 | 1 |
| Noctuinae | | |
| *Diarsia rosaria* | 0 | 1 |
| *Agrotis volubilis* | 0 | 1 |
| Geometridae | | |
| Ennomiinae | | |
| *Digrammia californiaria* | 1 | 0 |
| *Synaxis cervinaria* | 1 | 0 |
| *Eupithecia* sp. | 0 | 1 |
| Pyralidae | | |
| Phycitinae | | |
| *Zophodia grossulariella* | 0 | 24 |

## Discussion

Results of this study show that several species of moths, bees, wasps, and flies, visit flowers of

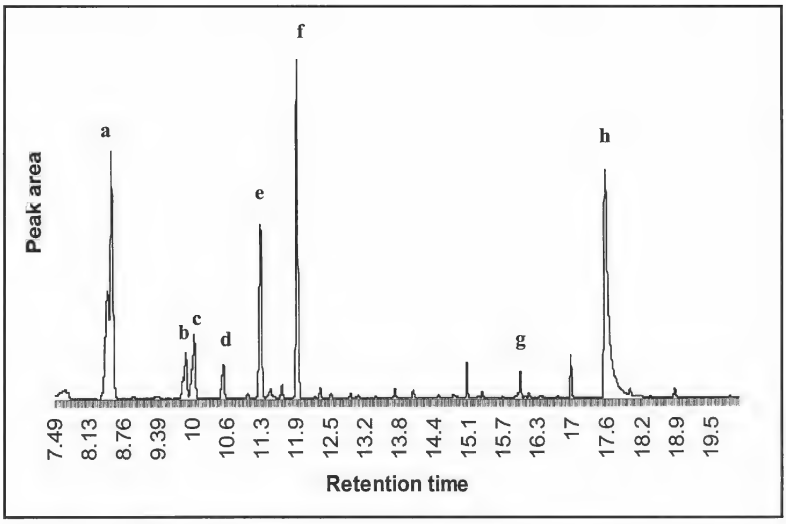


Figure 1. Typical chromatogram from analysis of volatile collection made over flowers of Oregongrape, using a DB wax capillary column. Peaks: (a) α-pinene, (b) β-pinene, (c) sabinene, (d) β-myrcene, (e) limonene, (f) E-β-ocimene, (g) benzaldehyde, and (h) phenylacetaldehyde.

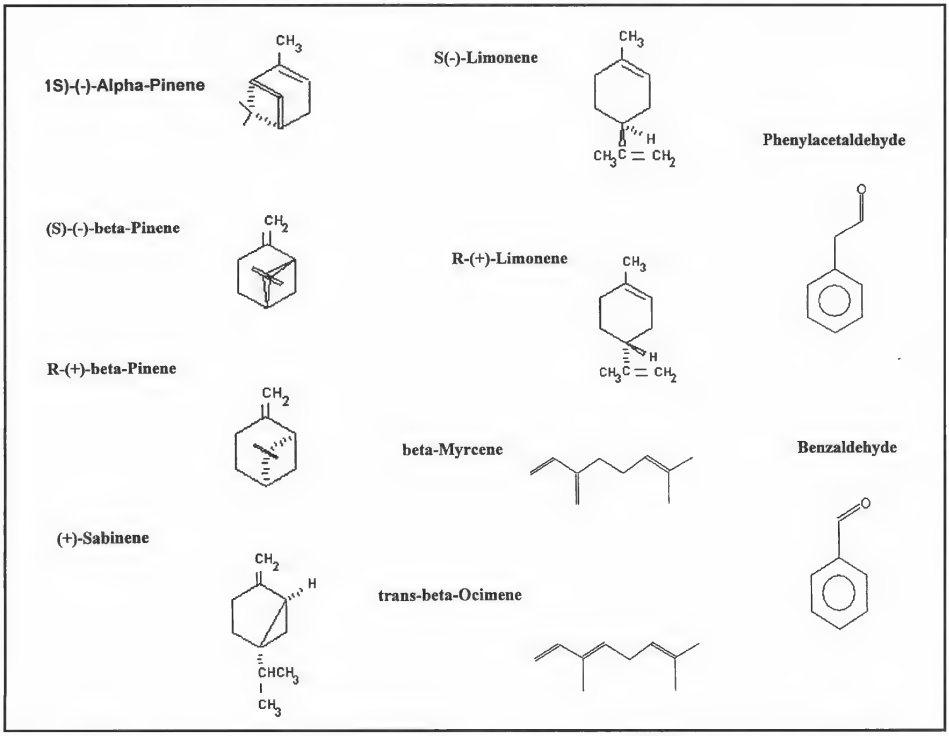


Figure 2. Structures of compounds isolated and identified from volatile collections made over open flowers of Oregongrape.

TABLE 2. Mean (± SE) nanograms of compounds emitted per Oregongrape flower per hour. N is the number of volatile collections from flowers from which quantitative data were obtained. α-Pinene and benzaldehyde co-eluted on two of five collections and were not quantified in those samples.

| Chemical | Nanograms | Percent of Total Emission | N |
|---|---|---|---|
| Phenylacetaldehyde | 124.5 ± 40.8 | 32.9 ± 2.0 | 5 |
| α-pinene | 87.6 ± 6.7 | 25.5 ± 6.4 | 3 |
| E-β-Ocimene | 54.4 ± 17.8 | 13.9 ± 2.8 | 5 |
| Limonene | 43.9 ± 7.0 | 12.5 ± 0.7 | 5 |
| Sabinene | 17.0 ± 2.7 | 4.9 ± 0.4 | 5 |
| Benzaldehyde | 14.5 ± 6.7 | 4.2 ± 6.7 | 3 |
| β-pinene | 12.3 ± 2.0 | 3.6 ± 0.4 | 5 |
| β-Myrcene | 8.6 ± 2.1 | 2.4 ± 0.3 | 5 |

Oregongrape and are potential pollinators. The most common moth visitor collected was the alfalfa looper moth. While both sexes of this moth were captured, the preponderance of alfalfa looper moths in traps were male. This species is generally abundant and flies from early spring into late autumn. Like the related cabbage looper and gamma moths, both male and female alfalfa looper moths visit flowers for nectar. The second most abundant moth collected was the gooseberry fruitworm moth. All collected specimens were female, suggesting that the moth may respond to Oregongrape flower chemicals in search of a place to oviposit, rather than in search of nectar on which to feed. However, this species is not known to infest fruits of Oregongrape. The makeup of the species of moths collected is likely influenced by the early-season blooming of Oregongrape in relation to the phenology of local moths, and by the regional moth community. Moths that emerge later in the season do not coincide with Oregongrape blooming, and the species of moths visiting Oregongrape flowers is probably somewhat different in other areas of the Pacific Northwest.

These data support the hypothesis that Oregongrape releases floral odorants attractive to moths. The odorous nature of Oregongrape flowers suggests that volatile chemicals are released that might attract some species of moths. This phenomenon is known for bladderflower (Cantelo and Jacobson 1979), glossy abelia (Haynes et al. 1991), night-blooming jessamine (Heath et. al. 1992), Drummond's gaura (Teranishi et al. 1991, Lopez et al. 2000), lesser butterfly orchid (Plethys 2001), and Japanese honeysuckle (Pair and Horvat 1997). Moths visit flowers of these plants and the flowers of the plants produce volatile chemicals that attract moths. Phenylacetaldehyde, which strongly attracts both sexes of the alfalfa looper (Landolt et al. 2001), is a major component of the floral odor of Oregongrape. This evidence suggests that alfalfa looper moths, and possibly other moth species, locate Oregongrape flowers by tracking the floral odor. It remains to be determined if other Oregongrape odor chemicals attract alfalfa looper moths.

The blend of chemicals collected over Oregongrape flowers includes phenylacetaldehyde and benzaldehyde, which are released by other moth-visited plants (Cantelo and Jacobson 1979, Haynes et al. 1991, Heath et al. 1992, Schlotzhauer et al. 1996). Phenylacetaldehyde is attractive to several species of moths, including the cabbage looper, the soybean looper (*Pseudoplusia includens*), and the alfalfa looper (Cantelo and Jacobson 1979, Haynes et al. 1991, Landolt et al. 1991, Heath et al. 1992, Pair and Horvat 1997). Phenylacetaldehyde and benzaldehyde occur in the hairpencils of males of some moths (Aplin and Birch 1970, Bestmann et al. 1977, Clearwater 1972, Grant et al. 1972). However, they are not known to play any pheromonal role in moth sexual interactions.

The floral bouquet of Oregongrape also includes a set of terpene compounds that are found in plant foliage and as plant odorants, but are not known to be moth attractants or moth pheromones. For example, β-pinene, limonene, (E)-β-ocimene, and myrcene are volatiles emitted from cotton plants (Pare and Tumlinson 1996), α-pinene, β-pinene, sabinene, limonene and (E)-β-ocimene are emitted from maple leaves (Loughrin et al. 1997), and α-pinene, β-pinene, sabinene, myrcene, and limonene are released from foliage of cabbage and nasturtium plants (Geerviliet et al.1997). These compounds may be pheromones or kairomones for other types of insects. For example, α- pinene, β-pinene, myrcene, sabinene, and limonene are released by some bark beetles and may be part of their aggregation pheromones (Mayer and McLaughlin 1991). Comprehensive field-testing of these compounds, separately and in multi-component blends, will be required to determine any roles they may play in attracting moths or other potential pollinators to Oregongrape flowers.

## Acknowledgements

We thank H. H. Neunzig for identifying gooseberry fruitworm moths collected over Oregongrape flowers. E-β-ocimene was purified from basil oil by J. Alfaro and J. Brumley. Sabinene was kindly provided by Pherobank Inc., Wageningen, The Netherlands.

## Literature Cited

Aplin, R. T., and M. C. Birch. 1970. Identification of odorous compounds from male Lepidoptera. Experientia 26:1193-1194.

Bestmann, H. J., O. Vostrowsky, and H. Platz. 1977. Pheromones XII. Male sex pheromones of noctuids. Experientia 33:874-875.

Cantelo, W. W., and M. Jacobson. 1979. Phenylacetaldehyde attracts moths to bladder flower and to blacklight traps. Environmental Entomology 8:444-447.

Clearwater, J. R. 1972. Chemistry and function of a pheromone produced by the male of the southern armyworm *Pseudaletia separata*. Journal of Insect Physiol. 18:781- 789.

Fleisher, Z., and A. Fleisher. 1992. Volatiles of *Ocimum basilicum* traditionally grown in Israel. Journal of Essential Oil Research 4:97-99.

Geerviliet, J. B. F., M. A. Posthumus, L. E. M. Vet, and M. Dicke. 1997. Comparative analysis of headspace volatiles from different caterpillar-infested or uninfested food plants of *Pieris* species. Journal of Chemical Ecology 23:2935-2954.

Grant, G. G. 1971. Feeding activity of adult cabbage loopers on flowers with strong olfactory stimuli. Journal of Economic Entomology 64:315-316.

Grant, G. G., U. E. Brady, and J. M. Brand. 1972. Male armyworm scent brush secretion: identification and electroantennogram study of major components. Annals of the Entomological Society of America 65:1224-1227.

Haynes, K. F., J. Z. Zhao, and A. Latif. 1991. Identification of floral compounds from *Abelia grandiflora* that stimulate upwind flight in cabbage looper moths. Journal of Chemical Ecology 17:637-646.

Heath, R. R., P. J. Landolt, B. Dueben, and B. Lenczewski. 1992. Identification of floral compounds of night-blooming jessamine attractive to cabbage looper moths. Environmental Entomology 21:854-859.

Landolt, P. J., B. Lenczewski, and R. R. Heath. 1991. A lure and kill system for cabbage looper moths, *Trichoplusia ni* (Lepidoptera: Noctuidae). Journal of Economic Entomology 84:1344-1347.

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Landolt, P. J., T. Adams, H. C. Reed, and R. S. Zack. 2001. Trapping alfalfa looper moths (Lepidoptera: Noctuidae) with single and double component floral chemical lures. Environmental Entomology 30:667-672.

Lopez, J. D., Jr., T. N. Shaver, K. R. Beerwinkle, and P. D. Lindgren. 2000. Feeding attractant and stimulant for adult control of noctuid and/or other lepidopteran species. U.S. Patent 6,074,634. Issued June 2000. United States Patent Office, Washington, D. C.

Loughrin, J. H., D. A. Potter, T. R. Hamilton-Kemp, and M. E. Byers. 1997. Response of Japanese beetles (Coleoptera: Scarabaeidae) to leaf volatiles of susceptible and resistant maple species. Environmental Entomology 26:334-342.

Mayer, S. M., and J. R. McLaughlin. 1991. Handbook of Insect Pheromones and Sex Attractants. CRC Press, Boca Raton.

Özek, T., H. Beis, B. Demircakmak, and K. H. C. Baser. 1995. Composition of the essential oil of *Ocimum basilicum* L. cultivated in Turkey. Journal of Essential Oil Research 7: 203-205.

Pair, S. D., and R. J. Horvat. 1997. Volatiles of Japanese honeysuckle flowers as attractants for adult Lepidopteran insects. U.S. Patent 5,665,344. Issued 9 September 1997. United States Patent Office, Washington, D.C.

Pare, P. W., and J. H. Tumlinson. 1996. Cotton volatiles synthesized and released distal to the site of insect damage. Phytochemistry 47:521-526.

Peck, M. E. 1961. A Manual of the Higher Plants of Oregon. Metropolitan Printing Company, Portland, Oregon.

Plethys, D. 2001. Odour-mediated nectar foraging in the silver Y moth, *Autographa gamma*. Ph.D. Dissertation, Lund University, Lund, Sweden.

Schlotzhauer, W. S., S. D. Pair, and R. J. Horvat. 1996. Volatile constituents from the flowers of Japanese honeysuckle. Journal of Agriculture and Food Chemistry 44:206-209.

Teranishi, R., R. G. Buttery, S. Kent, G. Takeoka, P. D. Lingren, J. R. Raulston, and T. N. Shaver. 1991. Chemical composition of *Gaura drummondii* flower volatiles. Journal of Essential Oil Research. 3:287-288.

# Northwest Science Notes

*The purpose of Notes is to publish papers typically less than five pages long. No specific format or content is required for articles published as Notes, but all will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.*

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## Non-native Blister Rust Disease on Whitebark Pine at Crater Lake National Park

### Abstract

Crater Lake National Park supports one of the largest aggregations of whitebark pine in the southern Cascades. The pine is valued by Park visitors and is considered a keystone species in local ecosystems. Although white pine blister rust has been in the region since the early 1900s, no formal survey of whitebark pine infection in the Park has been conducted to date. We sampled 1,200 whitebark pine trees with 24 transects to measure incidence of disease and other damaging agents in the Park. Blister rust is currently the most ubiquitous source of mortality for the Park's pines, outweighing all other biotic agents combined. The National Park Service is initiating actions to conserve whitebark pine.

### Introduction

Whitebark pine (*Pinus albicaulis*) is an extremely valuable asset of the southern Cascades. This long-lived and hardy tree thrives at sites with harsh climatic forces. The pine's large and nutritious seeds are prized by wildlife including Clark's nutcrackers (*Nucifraga columbiana*), black bears (*Ursus americanus*), and golden-mantled ground squirrels (*Spermophilus lateralis*). Elk (*Cervus elaphus*), blue grouse (*Dendragapus obscurus*), and bats use trees for shelter. Their canopies support arboreal lichens and understory flora such as woodrush (*Luzula* spp.) and currants (*Ribes* spp.). Whitebark pines also stabilize soil and regulate snowmelt. These values are acknowledged by natural scientists in defining the tree as a keystone species (Tomback et al. 2001). Every year, nearly 500,000 people view southern Oregon's Crater Lake from its pine-clad rim where the picturesque trees are the subject of postcards, artwork, and exhibits.

Many pines at Crater Lake National Park have been suspected of dying from an introduced fungus (*Cronartium ribicola*) which causes the disease known as white pine blister rust. This pathogen arrived in western North America at British Columbia in 1910. Although blister rust can infect the other five-needled pines in the Park, [western white (*Pinus monticola*) and sugar pine (*P. lambertiana*)], whitebark pine is by far the most susceptible (Bingham 1972). Blister rust has proven lethal in other parts of North America where up to 90% mortality of whitebark pine has been estimated (Kendall 1994).

Understanding of blister rust on whitebark pine in the southern Cascades is rudimentary because of little formal investigation. The disease was documented in the vicinity of the Park as early as 1935 (US Department of Agriculture 1949), however, historic records of damage to whitebark pine are absent. Bedwell and Childs (1943) observed no diseased whitebark pine south of Mt. Jefferson. Correspondingly, Bachelor Butte, located about 110 km to the north, was reported to have very light incidence (Lueck 1980).

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Growing concern in the region (Juillerat 2000) combined with our increasing awareness of infection on sugar and white pines catalyzed a whitebark pine survey in the Park. Our objective was to detect and estimate the incidence of white pine blister rust on the Park's whitebark pine. For the purpose of this study, we define incidence as the percentage of trees within a sample that exhibits blister rust.

## Methods

Our study area consisted of Crater Lake National Park, Oregon (74,132 ha) which is located on the crest of the Cascades in southern Oregon (Figure 1). The mean January and July temperatures at Park Headquarters are 13.7°C and 29.6°C. The moderate seasonal extremes in temperature contrast with the precipitation. Approximately 70% of total amount occurs between November and March as snow, which usually accumulates to nearly 5 m. Whitebark pine populations are restricted to the upper elevational limits of the Park (2,800 – 3,600 m) on the rim of Crater Lake's caldera, Mount Scott, and several other peaks. Pure stands of trees occur above 3,240 m while lower stands are codominated by mountain hemlock (*Tsuga mertensiana*), and occasionally lodgepole pine (*Pinus contorta*) and Shasta red fir (*Abies x shastensis*). The eastern side of the Park is cooler and drier as affected by easterly movement of storm masses and a more continental climate.

We inventoried survey transects within the whitebark pine zone of the Park (Figure 1). Due to the patchy distribution of whitebark pine, we combined both random and non-random sampling. About half of the transect starting points and azimuths were not random because the pine was restricted to small tree islands and the narrow edges of craters where strict randomness would result in intersecting few pine individuals. Non-random transect starts were subjectively placed in central locations, that were surrounded by whitebark pine, ensuring a random azimuth would work. Non-random azimuths followed an elevational contour or the established Rim Trail. For tree islands, a random island was chosen from which a random transect azimuth was followed. Often, these transects extended over meadows to other tree islands. Transects had variable widths depending on the density of whitebark pine trees. Widths ranged from 5 to 30 m and lengths varied between 54 and 612 m.

The first 50 live and dead trees along each transect were measured for diameter at breast height (dbh), live crown ratio, canopy dominance, and damaging agents. We noted when whitebark pine occurred in clusters of same-aged individuals. When we determined that a pine had active or inactive canker(s), we recorded percent of crown killed, canker distance to main stem, canker height above ground, and an estimate of the age of the most recent canker based on bark decay. Where more than one canker occurred on a tree, we chose the active canker nearest the stem and base, respectively, to describe. Trees that supported only cankers lacking any apparent fungal activity as indicated by the absence of all external symptoms (fungal fruiting structures, seeping sap, orangish bark) were recorded as infected individuals and also noted as possible resistant individuals (Hoff 1992).

At every transect slope, aspect, and elevation were recorded. Slope and aspect were measured at each end of the transects. Dominant understory flora were identified and the presence of currant shrubs was noted. The beginning and ending of each transect was georeferenced using a handheld global positioning system receiver. Analysis consisted of calculating the proportion of trees infected with blister rust (incidence) at each transect. Because currant shrubs transmit the fungal spores to trees, we compared incidence between transects with and without the shrub. We used the non-parametric Mann-Whitney U-test, which is appropriate for comparing proportional data (i.e. incidence values) (Fowler and Cohen 1990).

## Results

We inventoried twenty-four transects totaling 1,200 whitebark pine trees. Blister rust was detected at all but three transects. The disease infected up to 20% of trees (Table 1). Disease was found on all size classes (<0.1 cm, 0.2 - 25.0 cm, and >25.0 cm) of pine at dbh. About 8% of trees >25 cm dbh were infected. Twelve percent of trees 0.1-24 cm dbh were infected. Nearly 3% of saplings (trees less than breast height) were infected. On many of the largest trees, more than one canker was observed. In addition to possessing active cankers, these trees often had deteriorating tops

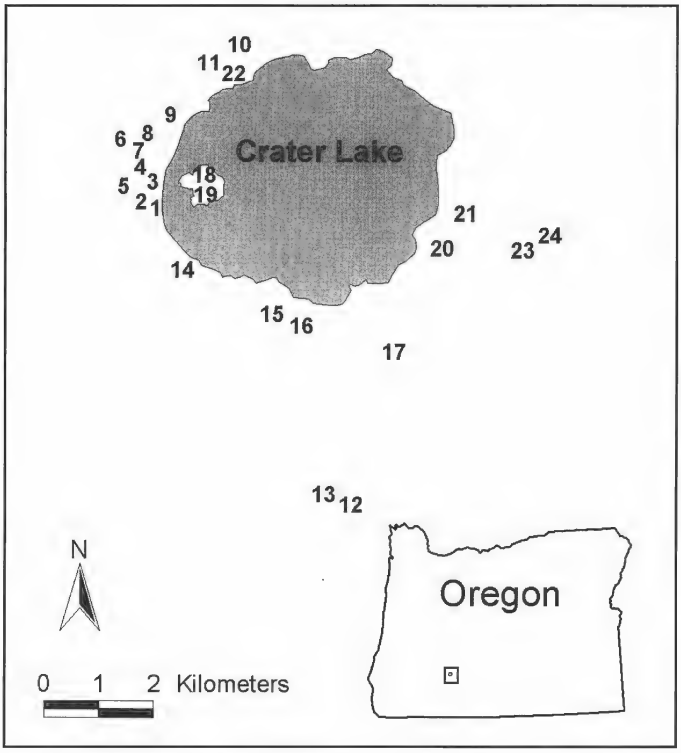


Figure 1. Location of twenty-four inventory transects within Crater Lake National Park, Oregon.

TABLE 1. Percentage of live trees (incidence) with blister rust on whitebark pine in Crater Lake National Park.

| Location | Transect No. | Trees Infected (%) |
|---|---|---|
| Rim Trail (Southern flank of The Watchman) | 1 | 20 |
| | 2 | 18 |
| Rim Trail (South of Discovery Point) | 14 | 18 |
| Williams Crater | 6 | 14 |
| | 7 | 18 |
| Hillman Peak | 8 | 14 |
| Applegate Peak | 16 | 12 |
| Devils Backbone (West of Rim Trail) | 9 | 12 |
| Llao Rock | 10 | 12 |
| | 22 | 4 |
| The Watchman | 3 | 10 |
| | 4 | 2 |
| | 5 | 4 |
| Crater Peak | 12 | 10 |
| | 13 | 4 |
| North Junction | 11 | 4 |
| Dutton Ridge | 17 | 8 |
| Cloudcap | 21 | 2 |
| Garfield Peak | 15 | 2 |
| Wizard Island | 18 | 2 |
| | 19 | 2 |
| Castle Rock | 20 | 0 |
| Mount Scott | 24 | 0 |

that appeared to have been dead for years. Trees possessing only inactive or dead cankers were rare, accounting for 0.67% of sampled trees. Additional agents of mortality were mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoe (*Arceuthobium* sp.), whose incidence was restricted to less than 2%, all on the summit of Wizard Island.

The 11 transects with currants supported significantly greater incidence of blister rust. Transects without currants averaged 4% infection while currant-populated transects averaged 12% infection.

## Discussion

Blister rust poses a long-term threat to the Park's whitebark pine populations. This disease is currently the most copious source of mortality in the Park's pines outweighing all other biotic agents combined. The most rapidly declining populations are along the west caldera rim. The low incidence of rust on the east side of the Park may be related to a cooler, drier weather pattern that can limit the pathogen's abundance (Hoff and Hagle 1990). The absence of currant shrubs from all eastern transects may further limit spread.

Annual loss is difficult to estimate without regular fixed-plot monitoring. Based on tallies of trees >7 cm dbh killed during the past year, we estimate the current rate of mortality on the western rim at 0.7% per yr. Taking into account an optimistic estimate of 0.3% recruited mature trees every year, based on our inventory of size classes, we predict an overall decline of 0.4% for mature trees annually. We can assume that the fungus has infected the Park's whitebark pine since its detection on other trees in the area during 1935 (USDA 1949). Therefore, at 0.4% annual loss current conditions may represent an overall shortfall of trees by 26% since 1935. That is, we would expect 26% more live and mature whitebark pine trees today. This gradual decline will become more pernicious as time passes. At the current rate, within 50 yr, there will be 20% fewer whitebark pine on the western rim than today. This value is about half of the historical abundance.

Our estimates of whitebark pine decline should be considered conservative. A separate survey in the Park during 2000 estimated 32-67% incidence (Ellen Goheen, USDA Forest Service, Medford, personal communication) with a lower sample size. Moreover, cankers are not easily distinguished on the oldest and youngest trees. Large trees support thick coverings of lichens that conceal the bark while cankers on seedlings are not reliably swollen.

As both a keystone species in Park habitats and a resource valued by the visiting public, the pine's precarious status warrants managerial attention. Park staff have initiated mapping, long-term monitoring, research, and disease resistance testing as preliminary steps towards protecting and restoring these valuable trees.

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## Literature Cited

Bedwell, J. L., and T. W. Childs. 1943. Susceptibility of whitebark pine to blister rust in the Pacific Northwest. Journal of Forestry 41:904-912.

Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines. Pages 271-280 *In* R.T. Bingham, R. J. Hoff, and G. McDonald (editors), Biology of Rust Resistance in Forest Trees. U.S. Department of Agriculture Miscellaneous Publication 1221, Washington, D.C.

Fowler, J., and L. Cohen. 1990. Practical Statistics for Field Biology. Wiley, New York.

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. USDA Forest Service Research Note INT-406. Intermountain Research Station, Ogden, Utah.

Hoff, R., and S. Hagle. 1990. Diseases of whitebark pine with special emphasis on white pine blister rust. Pages 179-190 *In* W. C. Schmidt and K. J. McDonald (compilers), Proceedings—Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-mountain Resource; 1989 March 29-31; Bozeman, Montana. USDA Forest Service General Technical Report INT-270. Intermountain Research Station, Ogden, Utah.

Juillerat, L. 2000. 'Gray ghosts' haunt Wizard Island. Klamath Falls Herald & News. 19 September 2000.

Kendall, K. C. 1994. Ecological mapping of whitebark pine in Glacier National Park. Pages 51-62 *In* K. C. Kendall and B. Coen (editors), Proceedings—Workshop on Research & Management in Whitebark Pine Ecosystems; 1994 May 3; West Glacier, Montana. Unpublished report on file at Glacier National Park.

Lueck, D. 1980. Ecology of *Pinus albicaulis* on Bachelor Butte, Oregon. M.S. Thesis, Oregon State University, Corvallis, Oregon.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, D.C.

U.S. Department of Agriculture 1949. White pine blister rust control in the northwestern region: January 1 to December 31, 1949. USDA Agricultural Research Administration, Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control. Government Printing Office, Washington, D.C.

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# NORTHWEST SCIENCE

*Information for Authors*

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The Northwest Scientific Association represents the natural and social sciences in the Pacific Northwest. The pages of *Northwest Science* are open to original and fundamental research in the basic and applied natural and social sciences. All submissions are refereed, usually by two reviewers and an Associate Editor. Papers are welcome from authors outside of the Pacific Northwest.

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Articles present the results of new and original research, and generally are 6–20 journal pages long. Authors must contact the Editor in advance before submitting longer papers. Authors are encouraged to use line numbering for the original submission, which will help speed up the review process.

## Notes

The purpose of Notes is to publish papers typically less than five journal pages long. Suggested topics include preliminary results, new methods, significant range extensions, and perhaps taxonomic observations. There is no specific format or content required for Notes, but all will be peer-reviewed and must be scientifically creditable. Authors may contact the Editor about the suitability of manuscripts to be published as Notes.

## Northwest Science Forum

This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum may not be peer-reviewed so that publication is expedited. The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

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- Literature Cited
- Footnotes
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- Figure Captions
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Cêska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

### *Monographs or books*

Edmunds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, New York. *(number of pages unnecessary)*

Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.

### *Papers in proceedings or symposia*

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pages 363-393 *In* H. Barnes (editor), Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, UK.

Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

### *Theses, dissertations, and articles in press*

Donald, D. B. 1971. The limnology of the plankton of three temporary ponds in Alberta. M.S. Thesis, University of Calgary, Calgary, Alberta.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. Ph.D. Dissertation, University of Utah, Salt Lake City, Utah.

Dunwiddie, P. W. *In Press*. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science. *(if the publication date is unknown or uncertain)*

Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecological Applications 10: *(in press). (if the publication date is known and certain).*

### *Technical bulletins*

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin Number 60. Washington State University.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

### *Online (web) references*

USDA Forest Service. 1998. Fire effects information system. Prescribed Fire and Fire Effects Research Work Unit, Rocky Mountain Research Station, Missoula, Montana. Available online at www.fs.fed.us/database/feis/

### *Unpublished Reports*

Unpublished reports often contain useful data that contribute to the development of the study being

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Revised July 2002

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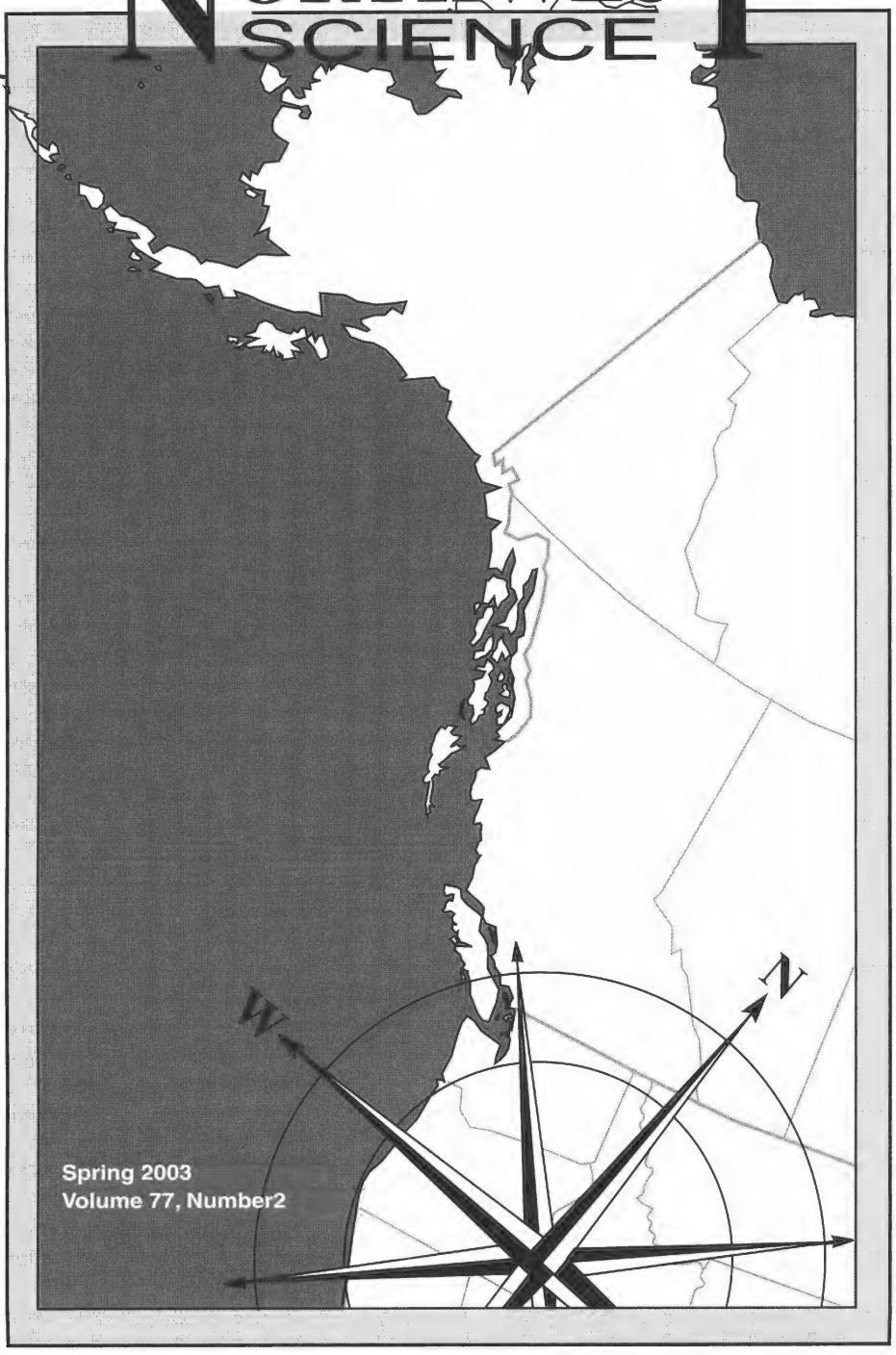


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(Founded 1923)

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Spring 2003 Volume 77, Number 2

# NORTHWEST SCIENCE


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*Information for Authors*

# Announcements

## 2003 Student Research Grant Awards

Each year the Northwest Scientific Association awards grants to several students who have submitted outstanding research proposals. Congratulations to this year's research grant winners, who were announced at the 2003 NWSA meeting in Forks, Washington:

- Paul Blanton, Central Washington University, "Arroyos in the Foster Creek watershed, Washington: an environmental reconstruction with management recommendations"
- Suzanne Griffin, University of Montana, "The decline of the Olympic marmot: evaluating spatial extent and causes"
- Aaron Hook, Portland State University, "Stormflow dynamics of dissolved organic carbon and total dissolved nitrogen in a small urban watershed"

Also in 2003, the first Ronald J. Taylor travel grant was awarded. This fund is designed to assist students who will present the results of outstanding research at the annual meeting. Congratulations to this year's travel winner, who was announced at the 2003 NWSA meeting in Forks, Washington:

- Joseph Rausch, Boise State University, "Genetic variation in the invasive grass *Taeniatherum caput-medusae* (Poaceae): randomly applied polymorphic DNA (RAPD) analysis"

**David H. Bennett,**[1] Department of Fish and Wildlife, University of Idaho, Moscow, Idaho 83844-1136
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and

**Craig A. Eaton,** Kooskia National Fish Hatchery, Route 1, Box 98a, Kooskia, Idaho 83539

# Substrate Composition and Emergence Success of Fall Chinook Salmon in the Snake River

## Abstract

The percentage of fine sediment particles in stream channel substrate is inversely related to emergence success of chinook salmon embryos. We used a previously published method to relate substrate composition at seven fall chinook salmon spawning sites in the Snake River implicitly to emergence success. We used dome suction to sample substrate at four spawning sites in the upper reach of Snake River and three in the lower reach. Mean percent fines < 6.4 mm and < 0.85 mm were less in upper reach samples than in lower reach samples. In laboratory tests, mean emergence success decreased from 47% to 10% as the mixtures of percent fines < 6.4 mm and < 0.85 mm increased in substrate mixtures. A regression equation developed from the laboratory data to predict mean emergence success from mean percent fines < 6.4 mm and < 0.85 mm had an $r^2$ value of 0.94. Predicted emergence success based on substrate composition in the Snake River ranged from 46% to 48% for sites in the upper reach, and from 29% to 47% for sites in the lower reach. These predictions of emergence success are slightly higher than those reported in the literature for chinook salmon spawning habitat. Based on the combination of field and laboratory findings, we conclude that substrate composition at the seven spawning sites we studied in the Snake River should not limit fall chinook salmon production.

## Introduction

During spawning, adult chinook salmon (*Oncorhynchus tshawytscha*) excavate nests in the stream bed referred to as redds. Substrate particle size in combination with certain hydraulic conditions are required to provide an ideal environment for redd construction and the incubation of chinook salmon embryos (Reiser and Bjornn 1979). Snake River fall chinook salmon typically construct redds in relatively homogenous substrate with particle diameters of 2.5 to 15.0 cm, in water depths of 0.2 to 6.5 m, and mean water column velocities of 0.4 to 2.1 m/s (Groves and Chandler 1999).

High concentrations of fine sediments in channel substrates where redds are constructed can reduce the percentage of salmonid embryos that survive to emergence (hereafter, emergence success). The causal mechanisms for reduced emergence success associated with increases in fine sediments were reviewed in detail by Bjornn and Reiser (1991). Excessive fines in the substrate can decrease permeability and water velocity to embryos. Decreased flow through the substrate reduces oxygen availability to embryos and slows removal of toxic metabolic wastes. Fry can also be entrapped when fine sediments are lodged in substrate interstices (Waters 1995). Emergence success has been quantified in laboratory channels (McCuddin 1977, Tappel and Bjornn 1983) and in the field (Burner 1951, McNeil and Ahnell 1964); each method has its advantages and disadvantages (Chapman 1988).

In general to assess substrate quality, gravel samples are collected within spawning areas (Tappel and Bjornn 1983). Individual samples are shaken through a stack of U.S. standard sieves (mesh size decreases from the top to bottom sieve). The percentage of the material (by weight) that passes through each of the sieves is then calculated to describe the cumulative particle size distribution for each sample. The percentages are then averaged by sieve size for all samples collected at a site to represent spawning gravel quality. Tappel and Bjornn (1983) found that the mean percentages of material that passed through the 9.5 mm and 0.85 mm sieves (i.e., two of the finer sediments) could be used in a second-order regression equation to explain 93% of the observed variability in mean emergence success of chinook salmon fry in the South Fork Salmon River (Figure 1). The findings of Tappel and Bjornn (1983) allowed biologists to relate the percentage of fine sediments

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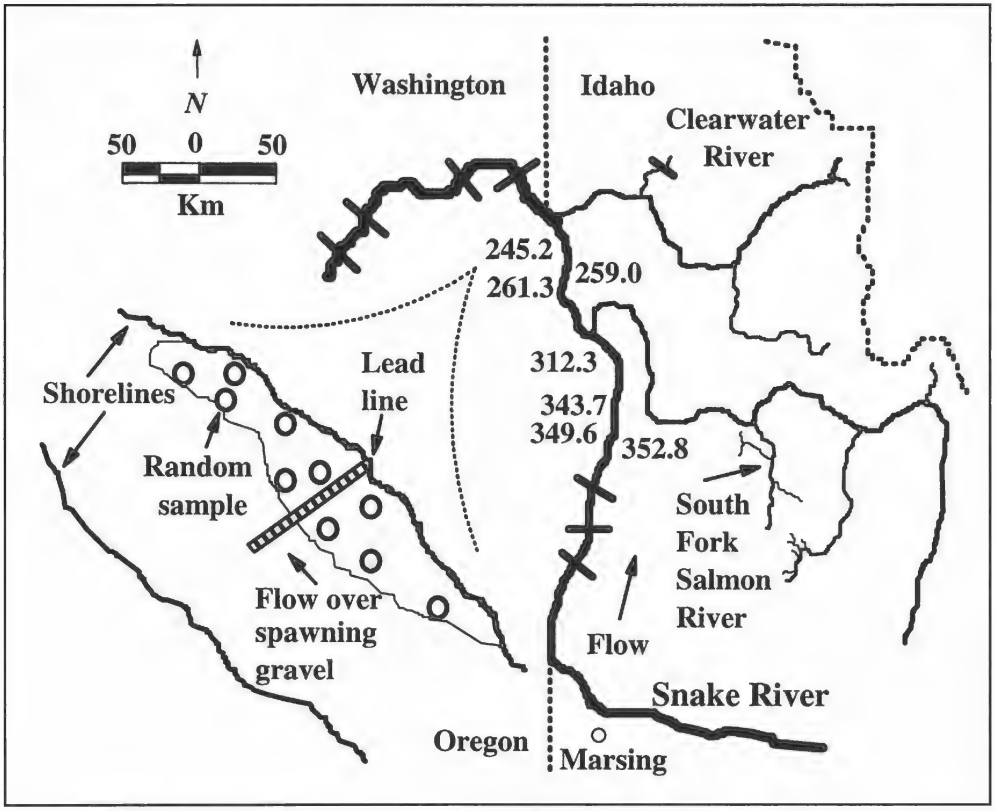


Figure 1. The Snake River where fall chinook salmon spawn including the approximate locations of our seven study sites (shown as the number of kms from the river mouth), the location of the South Fork Salmon River where Tappel and Bjornn (1983) conducted their study, and an inset showing an aerial view of the study site at rkm 245.2 with a marked lead line used to locate random substrate samples.

implicitly to emergence success by using only two particle sizes observed in substrate samples.

Information on substrate composition at fall chinook salmon spawning sites in the Snake River, and on emergence success at these sites, was needed to assess the potential for population recovery. A study on redd capacity indicated that the Snake River could support the 1,250 fall chinook salmon redds needed to meet the population recovery goal (Connor et al. 2001). When estimating redd capacity, however, it was assumed that substrate composition at fall chinook salmon spawning sites would not limit emergence success (Connor et al. 2001).

We use a modification of the method developed by Tappel and Bjornn (1983) to evaluate substrate composition at seven fall chinook salmon spawning sites in the Snake River. We report the results of laboratory tests on the effect of substrate composition on emergence success of fall chinook salmon embryos, and then use the laboratory findings to predict emergence success from the percentages of two sediment sizes measured in random substrate samples collected at the seven spawning sites.

## Study Area

Fall chinook salmon once spawned from Marsing Idaho to the Snake River mouth, but dam construction eliminated much of the historical spawning habitat (Figure 1). For a detailed description of the historical and present distribution of Snake River fall chinook salmon spawners and their habitat, we refer readers to papers by Groves and

Chandler (1999), Dauble and Geist (2000), Connor et al. (2001), and Garcia et al. (2001). The Snake River can be divided into three reaches based on differences in channel morphology and discharge. Between 1986 and 2000, there were 78 documented spawning sites in the upper reach, 11 in the middle reach, and 28 in the lower reach (Garcia et al. 2001). We studied four spawning sites in the upper reach and three in the lower reach. We identified sites by the distance they were located from the mouth of the Snake River (rkm).

## Methods

We obtained study site maps including the locations of redds and suitable-sized spawning substrate from Connor et al. (2001). We placed a numbered grid over each site map, and then selected 10 random sampling locations to depths utilized by spawners (Groves and Chandler 1999; Figure 1). In 1994 and 1995, divers identified the sample locations at each of the seven spawning sites in two steps. First, the distance the sample was located from the upstream edge of the gravel was measured along the shoreline. Second, the distance the sample was located offshore was measured by using a lead line marked at 10-m intervals placed perpendicular to the current (Figure 1). Substrate composition at each location was sampled by using a dome suction sampler (Gale and Thompson 1975).

Substrate samples were dried, weighed (g), and shaken through a U.S. standard sieve series (mesh sizes: 75, 50, 25.4, 12.5, 9.4, 6.4, 4.8, 3.4, 2.0, 0.85, 0.5, and 0.25 mm). The percentage of the substrate (by weight) in each sample that passed through each sieve was calculated as the weight of the material that passed divided by total sample weight. The sample results were used to calculate a mean percentage for each sieve size by spawning site. We selected the mean percentage of the substrate that passed the 6.4 mm and 0.85 mm sieves to relate the percentage of fine sediments to emergence success. We selected these particle sizes instead of 9.5 mm and 0.85 mm used by Tappel and Bjornn (1983) because mixtures of 6.4 mm and 0.85 mm sediments were well represented at the spawning sites and in our laboratory troughs.

We evaluated emergence success in the laboratory in 1996 by using eight substrate mixtures (Table 1) like those found in the seven spawning sites in the upper and lower reaches of the Snake River. Each of 48 wooden troughs (121.9 cm length x 30.5 cm wide x 30.5 cm deep) (Tappel and Bjornn 1983) was filled to a depth of 25 cm with one of the eight mixtures to provide six replicates per mixture. Each substrate mixture was labeled according to its percent fines < 6.4 mm and < 0.85 mm. Substrate mixtures were randomly assigned to each trough.

Eggs from three female and milt from five male fall chinook salmon were brought to our laboratory from Lyons Ferry Hatchery, Washington. To prevent bias resulting from differences in gamete viability, we fertilized the eggs in the form of a 3 X 5 matrix (female 1 with male 1, 2, 3, 4, and 5; female 2 with male 1, 2, 3, 4, and 5; female 3 with male 1, 2, 3, 4, and 5). The fertilized eggs were water hardened and then randomly mixed. We placed 50 fertilized eggs into each of two 25 cm depressions in the substrate, and then gently covered the eggs with ambient substrate

TABLE 1. Mean size composition of substrate mixtures (n=6 replicates per mixture) used in laboratory tests. Each substrate mixture is labeled according to the percent fines < 6.4 mm and < 0.85 mm. For example, 14:4 means that 14% of the mixture was smaller than 6.4 mm and 4% was smaller than 0.85 mm.

| Substrate Mixture | Percentage smaller than the given particle size | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 25.4 | 12.5 | 9.4 | 6.4 | 4.8 | 3.4 | 2.0 | 0.85 | 0.5 | 0.25 |
| 2:0 | 82.4 | 37.1 | 19.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 9:2 | 85.8 | 43.8 | 25.7 | 9.0 | 5.8 | 4.5 | 3.3 | 2.0 | 1.2 | 0.4 |
| 14:4 | 96.5 | 52.6 | 33.1 | 13.8 | 9.8 | 8.0 | 6.1 | 3.8 | 2.5 | 0.9 |
| 21.9 | 95.0 | 54.8 | 38.5 | 20.7 | 17.5 | 15.5 | 12.7 | 8.6 | 5.3 | 1.8 |
| 24:11 | 90.3 | 54.5 | 38.8 | 24.2 | 21.7 | 19.4 | 15.9 | 10.8 | 6.3 | 2.1 |
| 29:11 | 98.1 | 61.9 | 44.5 | 29.1 | 24.1 | 20.4 | 16.2 | 10.7 | 6.3 | 2.2 |
| 33:15 | 89.5 | 58.0 | 45.6 | 33.4 | 31.1 | 28.0 | 23.0 | 15.3 | 8.4 | 2.8 |
| 34:12 | 99.8 | 66.2 | 49.8 | 33.6 | 27.7 | 23.4 | 18.4 | 12.1 | 7.4 | 2.4 |

from the trough. Fungal (*Saprolegnia*) growths in troughs and control trays were treated with formalin.

Chilled, unchlorinated, recycled tap water flowed laterally through the troughs. Flows were regulated by ball valves and determined by gradient differences between the inflow and outflow sources. A 2% gradient was maintained where possible. Apparent velocity (cm/s) was measured weekly based on the volume of water passing through each trough. Dissolved oxygen (mg/L) was measured periodically with a YSI model 57 meter (Yellow Springs Instruments, Yellow Springs, Ohio) in perforated PVC pipe (20 cm long x 1.8 cm diameter) placed in the middle of each egg pocket nearest the outflow (9.78 mg/L = 100% saturation). Water temperatures were recorded hourly with a RTM 2000 meter (Ryan Tempmentor, Ryan Instruments, Redmond, Washington). We used ordinary least-squares regression to test the relation between mean percent fines < 0.85 mm, mean apparent velocity, and mean dissolved oxygen concentrations.

We removed and counted fry as they emerged from the substrate in each trough. We calculated emergence success in each trough as the proportion of fry that survived to emergence (n/100) and expressed this proportion as a percentage.

We used the data from our laboratory tests to develop second-order regression equations relating mean percent fines < 6.4 mm ($S_{6.4}$) and < 0.85 mm ($S_{0.85}$) to mean emergence success as described by Tappel and Bjornn (1983). Second-order terms ($S^2_{6.4}$, $S^2_{0.85}$) and a cross-product term ($S_{6.4}S_{0.85}$) were analyzed to account for the curvilinear relation between substrate particle size and emergence success. The best second-order regression model was selected based on $r^2$ values.

The last step of our analyses was to predict emergence success (± 95% prediction intervals) for embryos at each of the seven spawning sites. We made these predictions by using the mean values of percent fines < 6.4 mm and < 0.85 mm from the substrate samples collected at the sites into the best second-order regression equation.

## Results

Mean percent fines < 6.4 mm measured in the substrate samples from the seven spawning sites in the Snake River ranged from 6.7% to 19.8% (Table 2). Mean percent fines < 6.4 mm was lowest at rkm 312.3 and highest at rkm 245.1. Mean percent fines < 0.85 mm measured in the substrate samples ranged from 1.2% to 8.5% (Table 2). Spawning sites in the upper reach of the Snake River had consistently lower mean percent fines < 0.85 mm than spawning sites in the lower reach. No significant relationship was found between percent fines <0.85 mm and 6.4 mm.

TABLE 2. Mean percent fines (± SE) calculated from substrate samples collected at known fall chinook spawning sites (rkm) in the upper and lower reaches of the Snake River, Washington, in 1994 and 1995.

| | n | < 6.4 mm | < 0.85 mm |
|---|---|---|---|
| | | Upper Reach | |
| 352.8 | 10 | 13.6 ± 2.06 | 1.2 ± 0.25 |
| 349.6 | 10 | 11.0 ± 1.17 | 2.2 ± 0.34 |
| 343.7 | 10 | 6.7 ± 1.23 | 3.1 ± 0.25 |
| 312.3 | 10 | 7.5 ± 1.26 | 2.3 ± 0.50 |
| | | Lower Reach | |
| 261.3 | 10 | 15.3 ± 0.88 | 7.9 ± 0.70 |
| 259.0 | 9 | 9.7 ± 2.27 | 5.0 ± 1.30 |
| 245.2 | 10 | 19.8 ± 3.22 | 8.5 ± 1.55 |

Mean apparent velocities ranged from 0.96 cm/s in troughs with the 2:0 substrate mixture to 0.06 cm/s in troughs with the 34:12 substrate mixture. Apparent velocity was significantly negatively correlated with percent fines < 0.85 mm ($r$ = -0.93; $P < 0.001$). Mean dissolved oxygen concentrations ranged from 10.0 mg/L in troughs with the 2:0 substrate mixture to 9.7 mg/L in troughs with the 34:15 substrate mixture. The significant correlation between mean dissolved oxygen concentration and percent fines < 0.85 mm was negative and relatively low ($r$ = -0.71; $P$ = 0.048). Mean water temperature was similar among the troughs and increased seasonally during the experiment (mean, 9.5°C; range, 5.9 to 15.7 °C).

Mean emergence success in the laboratory troughs ranged from 7% to 51% (Table 3). Mean emergence success generally decreased as the mean percent fines < 6.4 mm and < 0.85 mm in the substrate mixtures increased (Table 3). The best second-order regression equation relating substrate composition to emergence success was: Emergence success = 46.643 + 1.194 $S_{0.85}$ – 0.111 $S_{6.4}S_{0.85}$ (r = 0.97; $P < 0.001$).

Predicted emergence success for embryos at the seven spawning sites in the Snake River was similar among sites, except for the relatively lower

TABLE 3. Mean predicted and observed emergence success (%, ± SE, n = 6 replicates per substrate mixture) and 95% confidence limits for fall chinook salmon in laboratory incubation troughs in 1996. Results are presented by substrate mixture according to percent fines <6.4 mm and <0.85 mm. For example, 14:4 means that 14% of the mixture was smaller than 6.4 mm and 4% was smaller than 0.85 mm.

| Substrate Mixture | Observed Emergence Success | Predicted Emergence Success | | |
|---|---|---|---|---|
| | | Predicted[1] | Lower Limit | Upper Limit |
| 2:0 | 51 ± 6.1 | 47 | 38 | 55 |
| 9.2 | 45 ± 4.5 | 47 | 41 | 53 |
| 14:4 | 39 ± 4.5 | 45 | 40 | 51 |
| 21:9 | 38 ± 4.1 | 36 | 30 | 43 |
| 24:11 | 34 ± 6.1 | 31 | 24 | 37 |
| 29:11 | 26 ± 6.9 | 24 | 20 | 29 |
| 33:15 | 7 ± 4.1 | 10 | 2 | 17 |
| 34:12 | 16 ± 6.1 | 16 | 9 | 23 |

[1]Emergence success = 46.643 + 1.194 $S_{0.85}$ – 0.111 $S_{6.4}S_{0.85}$ ($r$ = 0.97; $P$ < 0.001).

prediction for embryos at rkm 245.2 (Figure 2). Predicted emergence success of embryos ranged from 29% at rkm 245.2 to 48% at rkm 343.7.

## Discussion

These results validate the method developed by Tappel and Bjornn (1983) for implicitly relating substrate composition to emergence success of chinook salmon embryos. The regression equation reported here for predicting emergence success was also similar to the regression equation reported by Tappel and Bjornn (1983). Both equations included the term $S_{0.85}$ and a cross-product term ($S_{9.5}S_{0.85}$ or $S_{6.4}S_{0.85}$), and both equations explained over 90% of the variability in mean emergence success of chinook salmon embryos.

Mean percent fines < 6.4 mm and < 0.85 mm differed among substrate samples collected at fall chinook salmon spawning sites in the upper and lower reaches of the Snake River. Substrate samples collected at spawning sites in the upper reach of the Snake River contained consistently lower mean percent fines < 0.85 mm than sites in the lower reach. A similar, but less distinct pattern was also observed for mean percent fines < 6.4 mm. Overall, the levels of fine sediment in substrate samples from all seven spawning sites in the Snake River were below those known to adversely affect

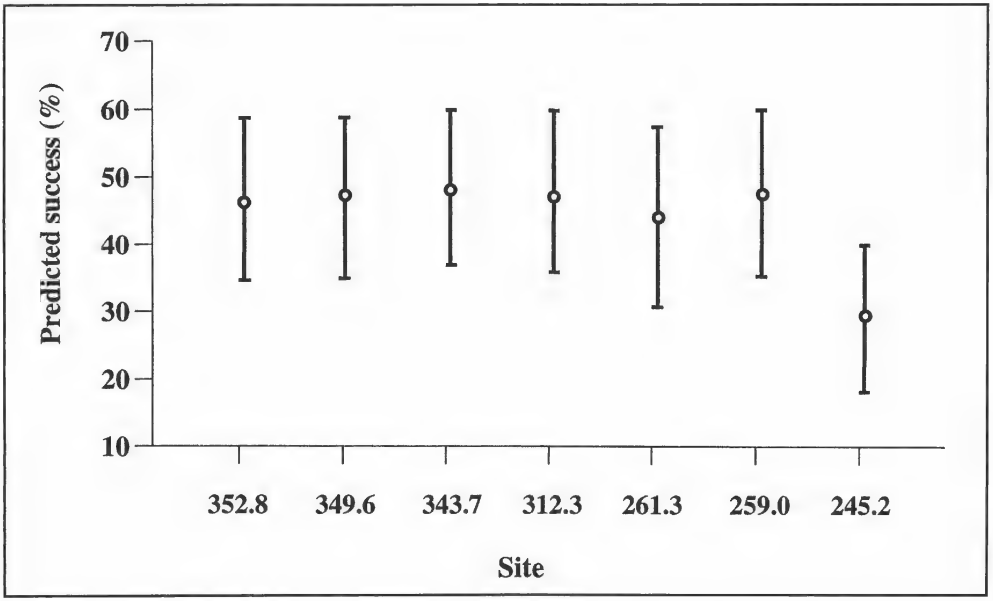


Figure 2. Emergence success (% ± 95% prediction interval) of fall chinook salmon embryos predicted from substrate composition of samples collected at each spawning site. Predictions were made by inputting the values for percent fines < 6.4 mm and < 0.85 mm for each site (Table 2) into the equation: Emergence success = 56.4 + 1.390 $S_{0.85}$ - 0.132 $S_{6.4}S_{0.85}$.

chinook salmon embryos (Bjornn 1969, McCuddin 1977, Chapman 1988, Bjornn and Reiser 1991).

Differences in sediment input and channel gradient are the most plausible explanations for differences in mean percent fines < 6.4 mm and < 0.85 mm in the substrate samples collected at spawning sites in the upper and lower reaches of the Snake River. The upper reach begins at Hells Canyon Dam (a sediment trap) (Goldman and Horne 1983), and the river in this reach does not receive sediment input from any large tributaries. Conversely, all of the spawning sites in the lower reach are located downstream of the Imnaha, Salmon, and Grande Ronde rivers. The channel gradient in the upper reach is also higher than in the lower reach (upper reach, 1.4 m/km; lower reach, 0.6 m/km) (Dauble and Geist 2000), which likely results in higher velocities and more efficient transport of fine materials.

Mean emergence success of fall chinook salmon embryos in our laboratory troughs decreased from 62% to 9% as mean percent fines < 6.4 mm and < 0.85 mm increased in the substrate mixtures. Dissolved oxygen concentrations in all troughs were above threshold levels for decreased embryo survival (Reiser and Bjornn 1979), yet the correlation between mean dissolved oxygen concentration and percent fines < 0.85 mm was significant. Also, apparent velocity was significantly correlated with percent fines < 0.85 mm, and apparent velocities measured in the substrate mixtures containing more than 10% fines < 0.85 mm were below safe thresholds for embryos survival (Reiser and Bjornn 1979). We found dead embryos entrapped in the substrate at termination of our experiment, but we could not count them because they were decomposed. We suspect mortality of embryos was largely related to the accumulation of toxic metabolites and embryo entrapment in the substrate.

The second-order regression equation we fit to relate substrate composition to mean emergence success of fall chinook salmon embryos predicted slightly higher emergence success at upper reach sites (mean, 47%) than at lower reach sites (mean, 40%). This difference was caused by relatively low emergence success predicted for embryos at rkm 245.2 (29%). In his definitive review of chinook salmon life history, Healey (1991) concluded that chinook salmon emergence success was roughly 30% in 13 rivers studied. Embryos in the wild have the advantage of an incubation environment modified by spawners to decrease levels of fine materials and maximize substrate permeability (Burner 1951, McNeil and Ahnell 1964, Chapman et al. 1986, Chapman 1988), whereas embryos in laboratory troughs have the advantage of disease treatment and an environment relatively free of organic sediments (Tappel and Bjornn 1983). Acknowledging the potential for differences in emergence success in the wild and in the laboratory, predicted emergence success of fall chinook salmon embryos at six of the seven spawning sites in the Snake River was high by comparison to the 30% level reported by Healey (1991). Based on the combination of field and laboratory findings, we conclude that substrate composition at the seven spawning sites we studied in the Snake River should not limit fall chinook salmon production.

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## Literature Cited

Bjornn, T. C. 1969. Embryo survival and emergence studies. Salmon and Steelhead Investigations, Job Completion Report, Project F-49-R-7. Idaho Department of Fish and Game, Boise, Idaho.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. American Fisheries Society Special Publication 19:83-138.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. U.S. Fish and Wildlife Service, Fisheries Bulletin 61:97-110.

Chapman, D. W., D. E. Weitkamp, T. L. Weish, M. B. Dell, and T. H. Schadt. 1986. Effects of river flow on the distribution of chinook salmon redds. Transactions of the American Fisheries Society 115:537-547.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids.

Transactions of the American Fisheries Society 117:1-21.

Connor, W. P., A. P. Garcia, A. H. Connor, E. O. Garton, P. A. Groves, and J. A. Chandler. 2001. Estimating the carrying capacity of the Snake River for fall chinook salmon redds. Northwest Science 75:363-371.

Dauble, D. D., and D. R. Geist. 2000. Comparison of mainstem spawning habitats for two populations of fall chinook salmon in the Columbia River Basin. Regulated Rivers: Research and Management 16:345-361.

Gale, W. F., J. D. Thompson, and J. Douglas. 1975. A suction sampler for quantitatively sampling benthos on rocky substrates on rivers. Transactions of the American Fisheries Society 104:398-405.

Garcia, A. P., R. D. Waitt, C. A. Larsen, D. Burum, B. D. Arnsberg, M. Key, and P. A. Groves. 2001. Fall chinook salmon spawning ground surveys in the Snake River basin upriver of Lower Granite Dam, 2000. Unpublished report on file at U. S. Fish and Wildlife Service, Idaho Fishery Resource Office, Ahsahka, Idaho.

Goldman, C. R., and A. J. Horne. 1983. Limnology. McGraw-Hill, New York.

Groves, P. A., and J. A. Chandler. 1999. Spawning habitat used by chinook salmon in the Snake River. North American Journal of Fisheries Management 19:912-922.

Healey, M. C. 1991. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). Pages 312-393 *In* C. Groot and L. Margolis (editors), Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, British Columbia.

McCuddin, M. E. 1977. Survival of salmon and trout embryos and fry in gravel-sand mixtures. M.S. Thesis, University of Idaho, Moscow, Idaho.

McNeil, J. W., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildlife Service Special Scientific Report Fisheries. No. 469.

Reiser, D. W., and T. C. Bjornn. 1979. Habitat Requirements of Salmonids in Streams. Pages 83-138 *In* W. R Meehan (editor), Influence of Forest and Rangeland Management on Salmonid Fishes and their Habitats. American Fisheries Society Special Publication 19, Bethesda, Maryland.

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3:123-135.

Waters, T. F. 1995. Sediment in Streams: Sources, Biological Effects and Control. Monograph 7. American Fisheries Society. Bethesda, Maryland.

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# Thermal Exposure of Juvenile Fall Chinook Salmon Migrating Through a Lower Snake River Reservoir

## Abstract

Impoundment of the Snake River, Washington, has resulted in high water temperatures and late seaward migration of juvenile fall chinook salmon during summer months. To determine if juvenile fall chinook salmon are exposed to temperatures higher than the upper incipient lethal, we tagged groups of fish with temperature-sensing radio tags and tracked them in Little Goose Reservoir on the Snake River during the summers of 1998 and 1999. Spatial and temporal patterns of the reservoir's thermal environment were described using a bathythermograph. Little Goose Reservoir was generally homothermic, and temperatures selected by fish were typically not significantly different from mean water temperatures. No areas of thermal refugia existed in Little Goose Reservoir. Thermal exposure was most influenced by fish residence time in the reservoir within each year and by temperature differences between years. Current augmentation of Snake River summer flows with cold-water releases from Dworshak Dam in Idaho reduces the thermal exposure of juvenile fall chinook salmon by lowering water temperatures up to 4°C and may therefore increase their survival. Continued flow augmentation using water from Dworshak Reservoir may be the only mechanism to meet the temperature standard for the lower Snake River.

## Introduction

The construction of Ice Harbor, Lower Monumental, Little Goose, and Lower Granite dams has impounded much of the lower Snake River, Washington. The only accessible free-flowing river reach is in Hells Canyon, located upstream of Lower Granite Reservoir. The Hells Canyon Reach supports a naturally-reproducing population of Snake River fall chinook salmon (*Oncorhynchus tshawytscha*), which is listed as threatened under the Endangered Species Act (National Marine Fisheries Service 1992). The timing of juvenile fall chinook salmon seaward migration is later than it was historically (Connor 2001), and fish currently emigrate through lower Snake River reservoirs in July and August when summer water temperatures are at a maximum.

The specific consequences of elevated thermal exposure to fish are currently unknown, but some general effects of warm water temperatures on juvenile chinook salmon are well documented. Among these is an increased risk of predation (Vigg and Burley 1991), disease (Fryer and Pilcher 1974; Holt et al. 1975), reduced gill $Na^+/K^+$ ATPase activity (a measure of smolt physiology that has been associated with migratory behavior in chinook salmon; Zaugg 1989; Beeman et al. 1991), and low survival and detections at dams (Muir et al. 1998; Connor et al. 1998). Finally, the upper incipient lethal temperature for juvenile chinook salmon is 24°C (Brett 1952), which was routinely exceeded in the top meter of the water column in Little Goose Reservoir.

Washington has established a maximum water temperature standard of 20°C for the lower Snake River to protect salmonids pursuant to the Clean Water Act (Washington Administrative Cod 1992). However, this standard is routinely exceeded during the summer migration of juvenile fall chinook salmon (U.S. Army Corps of Engineers 2002). As a consequence, the U.S. Army Corps of Engineers (operators of the federal dams on the lower Snake River) is currently in litigation for allegedly violating the temperature standards in the lower Snake River (132 S. Supp. 2d. 1072 (D.OR.2000)). The only short-term method to reduce these water temperatures is to release cold water from Dworshak Reservoir. This reservoir is located on the North Fork Clearwater River 68 km upstream of the Snake and Clearwater river confluence at Lewiston, Idaho (Snake River rkm 224) (Figure 1). However, the effect of Dworshak Reservoir releases on the thermal exposure of fish in the lower Snake River is unknown because thermal history information from migrants has not been available.

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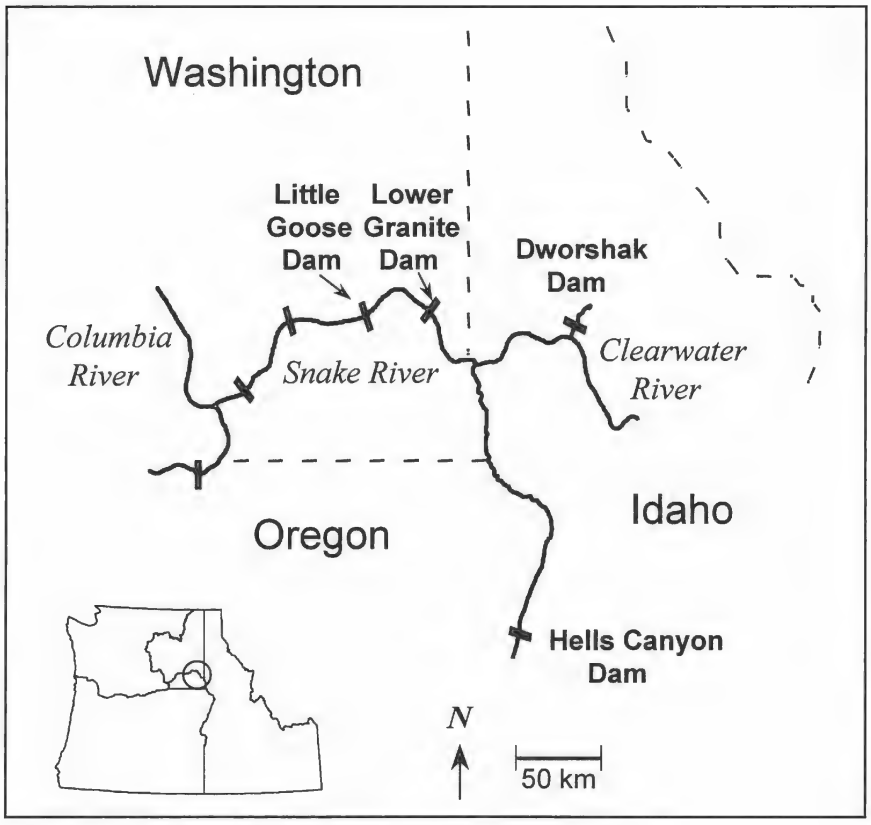


Figure 1. Study area showing Little Goose, Lower Granite, and Dworshak dams.

Areas of cool water (thermal refugia) may exist in lower Snake River reservoirs, which would allow fish to avoid temporarily unfavorably high temperatures (Karr et al. 1998). Monitoring stations that use thermographs may not adequately describe the temperatures experienced by fish migrating through the lower Snake River because inferences are limited to specific locations. Existing reservoir temperature data are relatively sparse and were usually collected at a crude spatial scale. The most complete data sets were collected from the scroll cases at the dams (Bennett et al. 1997, Karr et al. 1998). Temperatures measured at the dams or from single thermographs in the reservoirs cannot detect the presence of thermal refugia. The thermal environment at a finer spatial scale has not been adequately described for any of the lower Snake River reservoirs.

Thermal histories of juvenile fall chinook salmon migrating through lower Snake River reservoirs are also unavailable. However, recent advances in miniature electronics have resulted in temperature-sensing radio transmitters suitable for use in fish as small as 120 mm fork length. These tags make it possible to obtain thermal histories on migrating juvenile salmon. We used a combination of radio telemetry and temperature sampling to: (1) estimate the thermal exposure of juvenile fall chinook salmon migrating through a lower Snake River reservoir, and (2) to determine if selected temperatures differed from those generally available.

## Study Area

We conducted this study in Little Goose Reservoir located on the lower Snake River in eastern

Washington (Figure 1). The reservoir was created in 1970 with the completion of Little Goose Dam (River kilometer (rkm) 113 as measured from the Snake River mouth), and is approximately 60 km long. The reservoir has a mean width of 0.7 km and the mean depth increases from 14 to 32 m from the head of the reservoir to the forebay of Little Goose Dam. The reservoir has little storage capacity, low retention time (5.7 d at 1,416 $m^3/s$), and is operated as run-of-the-river for hydroelectric power generation. Discharges during the summer typically decline from about 2,266 to 566 $m^3/s$. Lower Granite Dam (rkm 173) is the only dam upriver of Little Goose Dam before the free-flowing Hells Canyon Reach, where Snake River fall chinook salmon adults spawn naturally and juveniles rear before migrating seaward.

## Methods

### Reservoir temperatures

The thermal environment of Little Goose Reservoir was characterized in 1998 and 1999 with a bathythermograph (BT) that continuously recorded time, depth, and temperature (accuracy = ±0.1°C). Twenty-five transects perpendicular to the longitudinal axis of the reservoir were established at roughly 2.5-km intervals from Little Goose to Lower Granite Dam. The BT was lowered at a rate of 0.4 m/s from the water surface to the bottom of the reservoir at five locations along each transect: south shoreline, 25% channel width (as measured from the south shore), 50% channel width, 75% channel width (as measured from the south shore), and north shoreline. Shoreline deployments were made as near as possible to the shore while staying within water 3-4 m deep. Data were collected from each transect at approximately 14-d intervals, which we refer to as time periods, from mid July to early September. For each profile, the BT temperature at the water surface was checked against the temperature measured with a mercury thermometer that met American National Standards Institute criteria. Equipment failure precluded collecting transect water temperature data during 5-19 July and 20 July-2 August 1999.

### Radio telemetry

Miniature temperature-sensing radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota) were used to collect thermal histories from juvenile fall chinook salmon. Transmitters were 17 mm long, 6 mm in diameter, weighed 1.7 g in air, and had a life span of 8 to 10 d. Tag accuracy was ±0.5°C. The transmitters operated on unique frequencies and had pulse intervals (in milliseconds) that varied directly and linearly with temperature. The manufacturer provided equations for each tag to convert pulse interval to temperature, which were validated along with tag performance in laboratory tests (Haskell et al. 1999). Because tags did not have a temperature sensor external to the fish, measured temperatures were those of the fish at any given time. The response time of the tags implanted in fish ranged from 2 min (0.5°C temperature change) to 4.5 min (6.0°C change), and varied directly with the magnitude of the temperature change (Haskell et al. 1999).

To obtain thermal histories from in-river migrants, we tagged naturally-produced juvenile fall chinook salmon collected at the Lower Granite Dam juvenile fish collection facility in 1998 and 1999. Fish selected for tagging were at least 120 mm fork length (FL), had no visible signs of injury or stress, and were unmarked indicating their natural origin. Fish were anesthetized in a 100 mg/L solution of buffered tricaine methanesulfonate (MS-222), weighed, and measured. A temperature-sensing radio transmitter was gastrically implanted in the fish as described by Adams et al. (1998a). After tagging, fish were allowed to recover for 24 hr before being released into the Lower Granite Dam tailrace via the PIT-tag bypass pipe in 1998 and by boat in the middle of the channel in 1999.

Totals of 69 and 76 juvenile fall chinook salmon were tagged with temperature-sensing radio transmitters and released into Little Goose Reservoir in 1998 and 1999. The mean size of radio-tagged fish ranged from 130 mm and 24.4 g to 176 mm and 73.7 g (Table 1). The ratio of the tag weight to fish body weight averaged 3.8% (range = 2.3 to 6.9%), which was less than the 5% limit used in other studies (Winter 1983, Adams et al. 1998a, Adams et al. 1998b). Tag retention during the 24-hr recovery period was 99% (one regurgitated tag each year), and there were no mortalities.

Groups of 5-7 tagged fish were released at regular intervals over five 9 to 14-d periods each year (Table 1). The fish with the strongest radio signal from each release group was tracked continuously for 48 hr by boat as it migrated through the reservoir. Fourteen fish were chosen as primary fish and intensively tracked in 1998. The mean number

TABLE 1. Release dates, number of fish (N), and mean fork lengths and weights, with standard errors in parentheses, of radio-tagged juvenile fall chinook salmon released into Little Goose Reservoir in 1998 and 1999.

| Release dates | N | Length (mm) | Weight (g) |
|---|---|---|---|
| **1998** | | | |
| 10-19 July | 14 | 138 (2.5) | 35.4 (2.0) |
| 20 July-1 August | 13 | 136 (2.7) | 33.3 (2.1) |
| 2-14 August | 14 | 142 (1.7) | 38.5 (1.5) |
| 15-28 August | 14 | 152 (2.1) | 46.7 (2.1) |
| 29 August-7 September | 14 | 167 (2.0) | 62.7 (2.4) |
| **1999** | | | |
| 5-19 July | 17 | 130 (7.5) | 24.4 (5.0) |
| 20 July-2 August | 11 | 144 (6.9) | 35.5 (4.8) |
| 3-15 August | 18 | 154 (4.7) | 44.1 (4.5) |
| 16-25 August | 12 | 161 (13.5) | 53.5 (13.7) |
| 26 August-4 September | 18 | 176 (7.1) | 73.7 (9.7) |

of temperature records collected per fish was 3,160 (range = 203 to 9,928). In 1999, 18 fish were intensively tracked, which had a mean number of temperature records per fish of 2,772 (range = 381 to 7,960). Other fish in the release groups were monitored to provide additional temperature information. If the primary fish was not detected for 4 hr, we tracked a different fish. Radiotag signals were detected with a data-logging receiver (Lotek Engineering Inc., Newmarket, Ontario, Canada) and a six-element Yagi antenna. Fish could only be detected to a maximum depth of 10 m due to radio signal attenuation. Each hour, the location of the selected fish was determined as the position of the strongest radio signal strength with a real-time differentially corrected global positioning system (GPS). In addition, a temperature profile of the water column was collected using a BT to compare mean fish and water temperatures subsequently at fish locations.

Fish movements and temperature exposures were also monitored by fixed-site receivers connected to stationary antenna arrays at Rice Bar (rkm 150) in 1999 only, New York Island (rkm 125), and the Little Goose Dam and forebay as described by Venditti et al. (2000). These arrays were used to corroborate data collected during boat tracking, monitor the movements and temperature exposures of tagged fish, and monitor temperature exposures of fish in the forebay of Little Goose Dam.

### Data Analysis

Mean water column temperatures were calculated for each BT transect and plotted to examine longitudinal and seasonal trends. Frequency histograms were constructed to determine the amount of temperature variation within BT profiles. To determine if fish and water temperatures were different, mean hourly temperatures for each fish were compared to mean BT temperatures at fish locations using paired t tests. Only fish with five or more detections were included in the analyses. Data were analyzed by time period and year.

Thermal exposure in cumulative daily temperature units (CTU) was calculated for each fish that passed Little Goose Dam. Exposure was calculated as the time (d) from a fish's release to its first detection at an exit site at Little Goose Dam multiplied by the mean reservoir temperature for that time period. High CTUs indicate greater temperature exposure. Mean exposures were compared between time periods within each year using analysis of variance and the Student-Newman-Kuels multiple range test. Within time period comparisons were made between years using two-tailed t-tests. All analyses were conducted using SAS statistical software (SAS 2000) and significance was designated at $P < 0.05$.

## Results

### Reservoir temperatures

Little Goose Reservoir showed similar trends in longitudinal temperature variation in both 1998 and 1999. Water temperatures were progressively higher from the tailrace of Lower Granite Dam to the forebay of Little Goose Dam (Figure 2). Mean BT-transect temperatures ranged from 19.5°C to 21.7°C in 1998 and from 17.6°C to 21.8°C in 1999. No individual water temperatures were <17.6°C in either year. The maximum water surface temperatures were 26.0°C in 1998 and 26.9°C in 1999. The highest water temperatures generally occurred in the top 1 m of the water column.

Mean temperatures in Little Goose Reservoir were generally >20°C in 1998 and were <20°C in 1999 (Figure 2). Seasonal variation in temperatures was greater in 1998, with the water temperatures in the upper third of the reservoir being the lowest during the latter half of July and highest in the lower half of the reservoir in early August

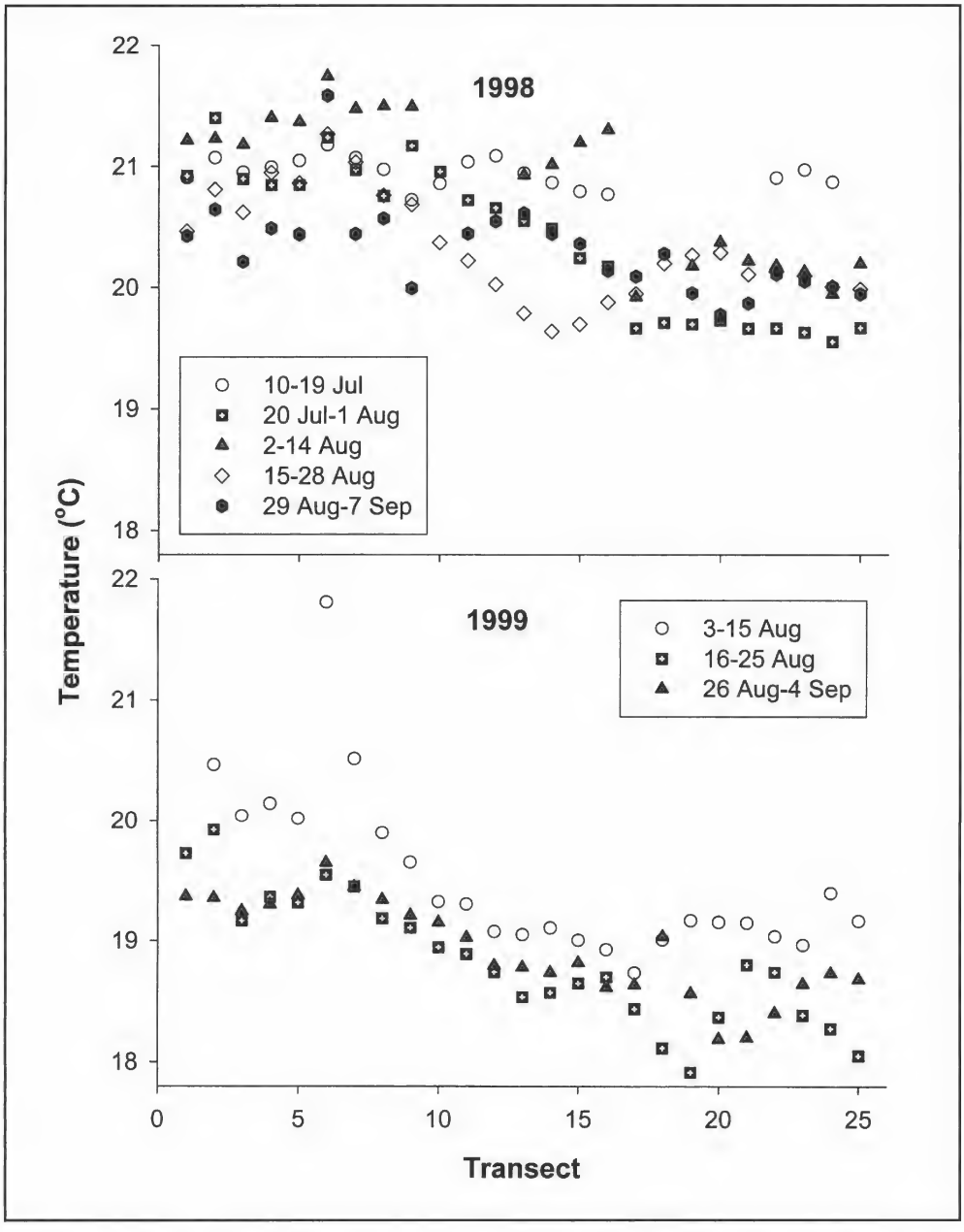


Figure 2. Mean temperatures as measured with a bathythermograph (BT) by transect and sampling period in Little Goose Reservoir in 1998 and 1999. Transects were spaced at approximately 2.5-km intervals and were numbered consecutively beginning with transect 1 in the Little Goose Dam forebay and ending with transect 25 in the Lower Granite Dam tailrace.

(Figure 2). Seasonal reservoir temperatures were less variable in 1999, and the entire reservoir averaged about 0.6°C higher during the first half of August than later in the year.

BT temperature profiles from Little Goose Reservoir showed that the water column was generally homothermic with no vertical stratification, except for higher temperatures in the top 1 m. We described the vertical thermal gradients in the water column using the frequency distribution of the differences between minimum and maximum water temperatures measured in BT profiles (Figure 3). Eighty-seven percent of the BT profiles in 1998 and 82% of the profiles in 1999 had maximum vertical temperature variations of 2°C or less. The greater temperature differences in Figure 3 were due to higher water temperatures measured near the surface.

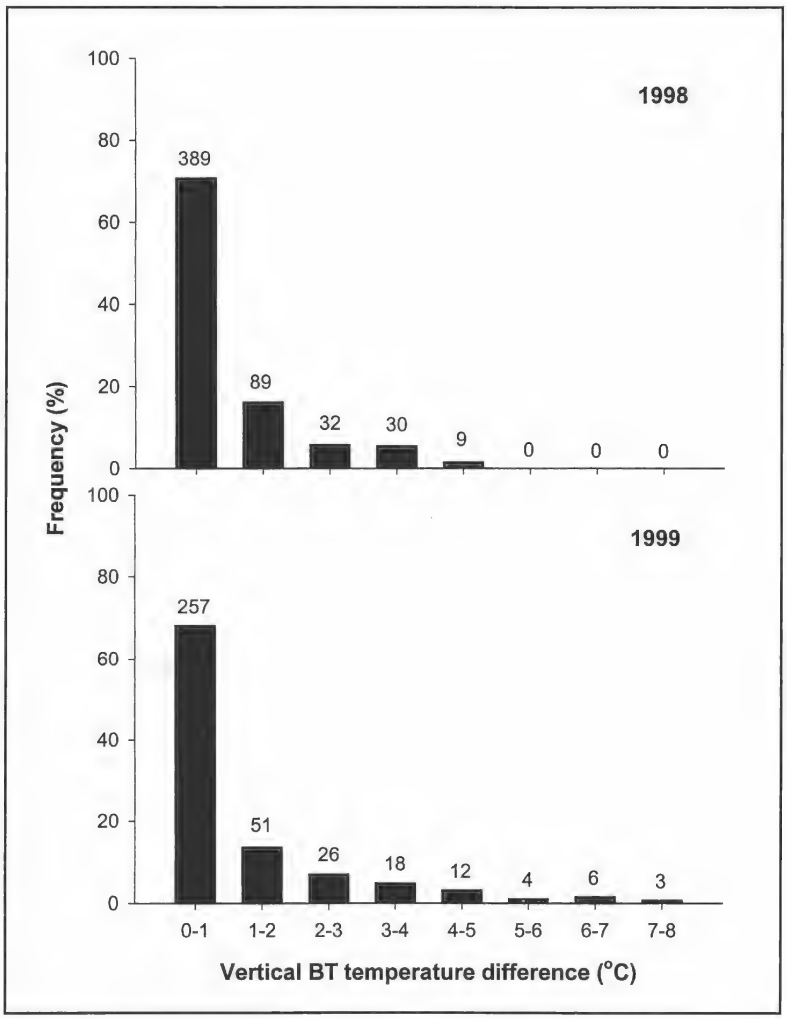


Figure 3. Percent frequency of maximum vertical temperature differences as measured with a bathythermograph (BT) in Little Goose Reservoir in 1998 and 1999. The numbers of BT profiles in each temperature-difference category are shown above each bar.

TABLE 2. Mean temperatures (°C) of juvenile fall chinook salmon fitted with temperature-sensing radio tags, and measured in Little Goose Reservoir with a bathythermograph (BT) at fish locations during 1998 and 1999. Means are summarized by time period.

| Time period | N | Mean fish temperature | Mean BT temperature | Temperature difference |
|---|---|---|---|---|
| **1998** | | | | |
| 10-19 July | 68 | 20.8 | 20.7 | 0.1 |
| 20 July-1 August | 12 | 20.9 | 20.8 | 0.1 |
| 2-14 August | 41 | 20.4 | 20.3 | 0.1 |
| 15-28 August | 8 | 20.6 | 20.5 | 0.1 |
| 29 August-7 September | 70 | 20.5 | 20.4 | 0.1 |
| **1999** | | | | |
| 5-19 July | 46 | 18.2 | 18.0 | 0.2 |
| 20 July-2 August | 60 | 19.5 | 19.2 | 0.3 |
| 3-15 August | 10 | 19.8 | 19.8 | 0.0 |
| 16-25 August | 58 | 19.5 | 19.2 | 0.3 |
| 26 August-4 September | 93 | 19.4 | 19.3 | 0.1 |

## Radio telemetry

The temperature histories of radio-tagged fish in Little Goose Reservoir were generally not significantly different from mean water column temperatures measured with a BT at fish locations (Table 2). Significant differences between mean temperature of fish and water were found in 4 of 10 t-test comparisons. However, differences between means ranged from 0.0°C to 0.3°C and averaged about 0.1°C (Table 2). This mean difference is less than the error associated with the tags thus we do not consider the differences biologically significant.

We calculated the thermal exposure of 90 fish detected in the Little Goose Dam forebay or at an exit site indicating that they had passed the dam. Thermal exposure of juvenile fall chinook salmon increased throughout the summer in 1998, but no trend was evident in 1999 (Figure 4). Significant differences existed between thermal

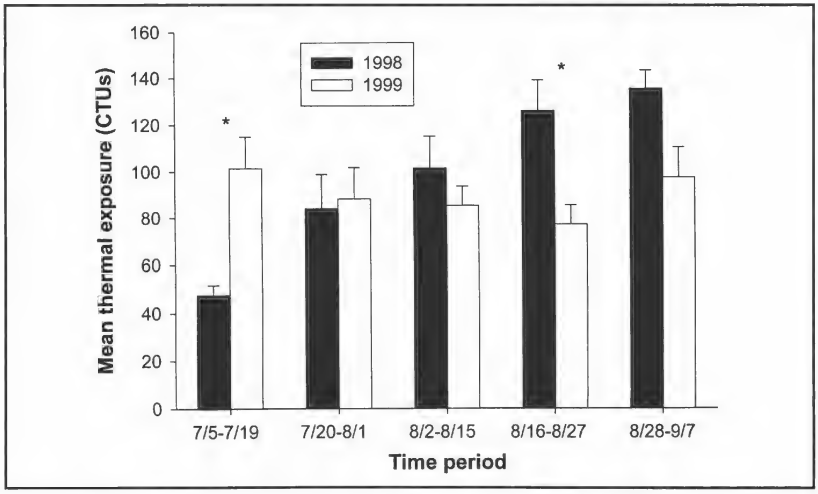


Figure 4. Mean thermal exposures of juvenile fall chinook salmon in Little Goose Reservoir by time period in 1998 and 1999. Thermal exposure is the product of fish residence time (d) in Little Goose Reservoir and the mean reservoir temperature for that time period. Standard error bars are shown. Significant ($P < 0.05$) between-year comparisons are denoted with asterisks.

exposures for different time periods in 1998 ($P$ = 0.0024). The exposure of fish from the early-July time period was significantly different from fish in late August and early September periods, but there were no significant differences between exposures after late July. No significant differences in seasonal exposures were found in 1999. Between-year comparisons showed that exposures were significantly different during early July ($P$ = 0.0120) and late August ($P$ = 0.0034) (Figure 4).

## Discussion

Temperature-sensing radio tags effectively provided thermal exposure data for juvenile fall chinook salmon migrating through Little Goose Reservoir. We used gastric, rather than surgical, implantation of tags because we believed it was less intrusive for the size of fish with which we worked. Although gastric implantation reduces long-term growth in juvenile salmonids (Adams et al. 1998b), there is less potential for short-term bias in swimming performance (Moser et al. 1990, Peake et al. 1997, Adams et al. 1998a). The fish tagged in this study behaved similarly and had migration rates similar to fall chinook salmon radio tagged and released in Little Goose Reservoir by Venditti et al. (2000).

Bathythermograph temperatures in Little Goose Reservoir showed that during the summers of 1998 and 1999 the reservoir was well mixed, exhibited no thermal stratification, and had no water temperatures <17.6°C. These data are similar to the findings of Bennett et al. (1997) who used a more coarse-scale temperature monitoring approach in the lower Snake River reservoirs in the early 1990s. Generally, fish did not have a wide range of temperatures from which to choose in Little Goose Reservoir, likely due to the low retention time of water in the reservoir, that contributes to well-mixed, homothermic conditions. Our comparisons of hourly fish temperatures and ambient water temperatures at fish locations revealed no biologically significant differences (Table 2). As a result, mean water column temperatures could be used as a surrogate for fish temperatures in Little Goose Reservoir and potentially for other main-stem reservoirs that are predominantly homothermic.

We found no evidence that thermal refugia existed in Little Goose Reservoir. We defined thermal refugia as having temperatures ≤17.8°C, which represents the maximum temperature preference for subyearling fall chinook salmon from the Columbia River (Sauter et al. 2001). The lowest temperature recorded by the BT or radio-tagged fish was 17.6°C, which was measured on a single occasion in mid August, 1999.

The thermal exposure of juvenile fall chinook salmon in Little Goose Reservoir was primarily influenced by residence time within each year and by temperature differences between years. In 1998, temperatures were relatively constant over the season (Figure 2), but fish residence times in the reservoir increased seasonally. Both residence times and temperatures exhibited little seasonal variation in 1999. Although temperatures were about 1°C lower overall in 1999 compared to 1998 (Figure 2), longer residence times for fish migrating early in 1999 contributed to their greater thermal exposures. Both higher temperatures and longer residence times in late 1998 resulted in higher exposures than in 1999.

During our study, water temperatures measured at Little Goose Dam exceeded the 20°C temperature standard for 56 d in 1998 but only for 4 d in 1999. These temperatures contributed in part to the greater thermal exposure experienced by fish in 1998. Two methods to reduce thermal exposure of juvenile fall chinook salmon in the lower Snake River are 1) to reduce residence times during migration or 2) to cool the reservoir water. Since 1992, fishery managers have attempted to do both, and thereby increase survival, by augmenting summer flows with cold-water releases from Dworshak Reservoir in Idaho. Flow augmentation not only reduces water temperatures, but also increases flow, which reduces fish travel time (Berggren and Filardo 1993). Connor (2001) used a one-dimensional heat budget model to compare observed and predicted water temperatures of the Lower Granite Reservoir tailrace in 1998 and 1999 both with and without flow augmentation from Dworshak Reservoir. Figure 5 summarizes his results, which show up to a 3-4°C reduction in summer water temperatures due to flow augmentation. Without the current temperature reduction that flow augmentation affords, thermal exposure of juvenile fall chinook salmon in the lower Snake River would be higher, and

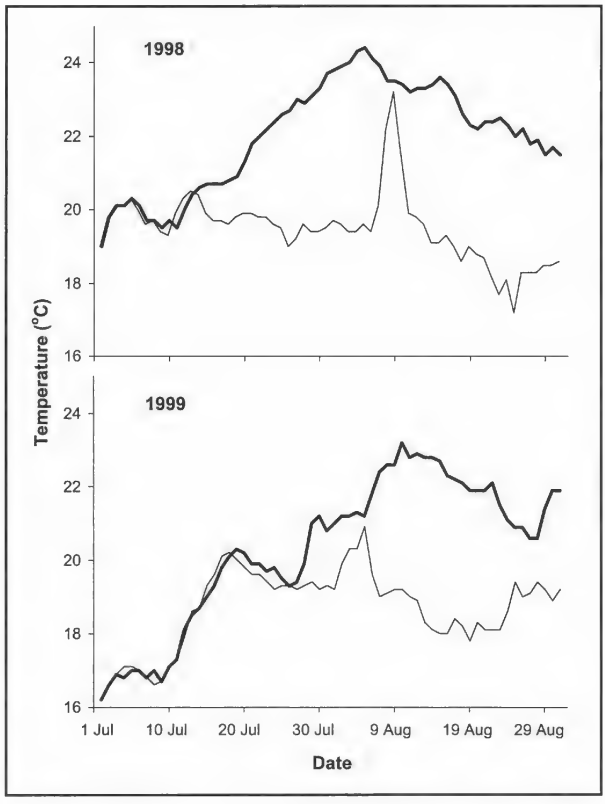


Figure 5. Mean daily observed (thin line) water temperatures in the Lower Granite Dam tailrace with flow augmentation from Dworshak Reservoir and those predicted (heavy line) without flow augmentation in 1998 and 1999. Observed temperatures were measured with a thermograph and predicted temperatures were obtained from a one-dimensional heat budget model (Yearsley et al. 2001). In 1998, flow augmentation began on 13 July and ended on 23 August, and in 1999, flow augmentation occurred from 19 July through 29 August. This figure was reproduced with permission from Connor (2001).

would potentially further reduce their survival. Continued flow augmentation using water from Dworshak Reservoir may be the only way to prevent the exceeding the temperature standard for the lower Snake River.

## Acknowledgments

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## Literature Cited

Adams, N. S., D. W. Rondorf, S. D. Evans, J. E. Kelly, and R. W. Perry. 1998a. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 55:781-787.

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998b. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile chinook salmon. Transactions of the American Fisheries Society 127:128-136.

Beeman, J. W., D. W. Rondorf, J. C. Faler, P. V. Haner, S. T. Sauter, and D. A. Venditti. 1991. Assessment of smolt condition for travel time analysis. Unpublished Annual Report to the Bonneville Power Administration, Contract DE-AI79-87BP35245, Portland, Oregon.

Bennett, D. H., M. H. Karr, and M. A. Madsen. 1997. Thermal and velocity characteristics in the lower Snake River reservoirs, Washington, as a result of regulated upstream water releases. Unpublished Final Completion Report

to the U.S. Army Corps of Engineers, Project 14-16-0009-1597, Walla Walla, Washington.

Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. North American Journal of Fisheries Management 13:48-63.

Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus Oncorhynchus. Journal of the Fisheries Research Board of Canada 9:265-322.

Connor, W. P., H. L. Burge, and D. H. Bennett. 1998. Detection of PIT-tagged subyearling chinook salmon at a Snake River dam: implications for summer flow augmentation. North American Journal of Fisheries Management 18:530-536.

Connor, W. P. 2001. Juvenile life history, downstream migration rate, and survival of wild Snake River fall chinook salmon. Ph.D. Dissertation. University of Idaho, Moscow, Idaho.

Fryer, J. S., and K. S. Pilcher. 1974. Effects of temperature on diseases of salmonid fishes. U.S. Environmental Protection Agency, Ecological Research Series EPA-660/3-73-020, Washington, D.C.

Haskell, C., D. Venditti, M. Tennier, and J. Kraut. 1999. Thermal exposure of juvenile fall chinook salmon migrating through Little Goose Reservoir, 1998. Pages 73-91 *In* K. F. Tiffan, D. W. Rondorf, W. P. Connor, and W. H. Miller (editors), Post-release attributes and survival of hatchery and natural fall chinook salmon in the Snake River. Unpublished Annual Report to the Bonneville Power Administration, Contract DE-AI79-91BP21708, Portland, Oregon.

Holt, R. A., J. E. Sanders, J. L. Zinn, J. L. Fryer, and K. S. Pilcher. 1975. Relation of water temperature to *Flexibacter columnaris* infection in steelhead trout (*Salmo gairdneri*), coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Journal of the Fisheries Research Board of Canada 32:1553-1559.

Karr, M. H., J. K. Fryer, and P. R. Mundy. 1998. Snake River water temperature control project, Phase II. Unpublished Report to the U.S. Environmental Protection Agency, Contract X-990375-01-1, Portland, Oregon, and the U.S. Department of Commerce, Contract WASC-6-2160, Portland, Oregon.

Moser, M. L., A. F. Olson, and T. P. Quinn. 1990. Effects of dummy ultrasonic transmitters on juvenile coho salmon. Pages 353-356 *In* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans (editors), Fish-marking techniques. American Fisheries Society, Bethesda, Maryland.

Muir, W. D., S. G. Smith, E. E. Hockersmith, M. P. Eppard, W. P. Connor, T. Andersen, and B. D. Arnsberg. 1998. Passage survival of natural and hatchery subyearling fall chinook salmon to Lower Granite, Little Goose, and Lower Monumental dams, 1996. Chapter 2 *In* J. G. Williams and T. C. Bjornn (editors), Fall chinook salmon survival and supplementation studies in the Snake River and lower Snake River reservoirs. Unpublished Annual Report to Bonneville Power Administration, Contracts DE-AI79-91BP21708 and DE-AI79-93BP10891, Portland, Oregon.

National Marine Fisheries Service. 1992. Threatened status for Snake River spring/summer chinook salmon, threatened status for Snake River fall chinook salmon. [Docket 910847-2043 22 April 1992] 57(78):14536-14663.

Peake, S., R. S. McKinley, D. A. Scruton, and R. Moccia. 1997. Influence of transmitter attachment procedures on swimming performance of wild and hatchery-reared Atlantic salmon smolts. Transactions of the American Fisheries Society 126:707-714.

SAS (Statistical Analysis System). 2000. SAS/STAT User's Guide, Release 8.1. SAS Institute, Inc., Cary, North Carolina.

Sauter, S. T., L. I. Crawshaw, and A. G. Maule. 2001. Behavioral thermoregulation by juvenile spring and fall chinook salmon, *Oncorhynchus tshawytscha*, during smoltification. Environmental Biology of Fishes 61:295-304.

U.S. Army Corps of Engineers. 2002. Columbia River Data Access in Real Time. Available online at www.cbr.washington.edu/dart/dart.html.

Venditti, D. A., D. W. Rondorf, and J. M. Kraut. 2000. Migratory behavior and forebay delay of radio-tagged juvenile fall chinook salmon in a lower Snake River impoundment. North American Journal of Fisheries Management 20:41-52.

Vigg, S., and C. C. Burley. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 48:2491-2498.

Washington Administrative Code. 1992. Water quality standards for surface waters of the state of Washington. Chapter 173-201A WAC. Olympia, Washington.

Winter, J. D. 1983. Underwater biotelemetry. Pages 371-395 *In* L. A. Nielsen and D. L. Johnson, editors, Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Yearsley, J., D. Karna, S. Peene, and B. Watson. 2001. Application of a 1-D heat budget model to the Columbia River system. Unpublished Final Report 901-R-01-001 by the U.S. Environmental Protection Agency, Region 10, Seattle, Washington.

Zaugg, W. S. 1989. Migratory behavior of underyearling *Oncorhynchus tshawytscha* and survival to adulthood as related to prerelease gill ($Na^+/K^+$)-ATPase development. Aquaculture 82:339-353.

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# Brook Stickleback Established in Eastern Washington

## Abstract

This note documents the first record of brook stickleback in Washington. Brook stickleback is established in the upper 36 km of Rock Creek, Spokane County, Washington. Rock Creek is a tributary of the Palouse River, which drains into the Snake River. Collections prior to 1999 yielded no brook stickleback in this drainage, leading us to believe that the species was recently introduced. This is the fifth record of occurrence west of the continental divide in the United States since 1995. Brook stickleback were previously collected in the Swan/Flathead River drainage, Montana, Green River drainage, Utah, Elk River drainage, Colorado and Klamath River drainage, California.

## Introduction

The purpose of this study was to document the recent invasion and distribution of brook stickleback (*Culaea inconstans*) in eastern Washington. The natural distribution of brook stickleback in North America was centered east of the Rocky Mountains, primarily in the upper Missouri/Mississippi River, Peace/McKenzie River, Great Lakes, and Hudson Bay drainages (Nelson 1969, Wooten 1976, 1984, Lee et al. 1980). Brook stickleback historically occurred on the eastern slopes of the Rocky Mountains in British Columbia (Scott and Crossman 1973), Alberta (Nelson and Paetz 1992), Northwest Territories (McPhail and Lindsey 1970) and Montana (Brown 1971, Holton and Johnson 1996), but not Wyoming (Baxter and Stone 1995).

Historically, brook stickleback were not reported west of the continental divide in North America (Jordan and Gilbert 1883; Gilbert and Evermann 1895; Jordan and Evermann 1896-1900; Jordan et al. 1930; Schultz and DeLacy 1935, 1936; Schultz 1936; Brown 1971; Wydoski and Whitney 1979; Simpson and Wallace 1982). Additionally, the only fossil stickleback reported west of the continental divide is *Gasterosteus* ( Miller 1958, 1965; Mural 1973).

Brook stickleback was first recorded west of the continental divide in 1991 in tributaries of the Klamath River, California (Moyle 2002). Brook stickleback specimens were later reported (1995) from the Green River, Utah (Modde and Haines 1996), Elk River, Colorado (Modde and Haines 1996), and Swan River, Montana (Holton and Johnson 1996). The Montana specimens were thought to have originated from an illegal introduction prior to 1995 and, by 1997, had extended their distribution downstream to Flathead Lake (Jim Vashro, Montana Department of Fish, Wildlife and Parks, Kalispell, Montana, personal communication). This paper documents the first record of brook stickleback in Washington State and the fifth record of its occurrence west of the continental divide.

## Methods

Brook stickleback were collected during routine electrofishing and dipnet surveys for fish and benthic invertebrates in the Rock Creek drainage, Spokane and Whitman Counties, Washington in 1999 and 2000 (Figure 1). Rock Creek arises on the Turnbull National Wildlife Refuge, 30 km southwest of Spokane and drains southwest into the Palouse River. The drainage is located in the channeled scablands geological province, formed by outburst floods from glacial Lake Missoula (Waite 1980). Study sites are presented in Figure 1. Latitude and longitude coordinates were obtained using a Garmin E-map Global Positioning System and confirmed using Terrain Navigator software. Brook stickleback were identified using

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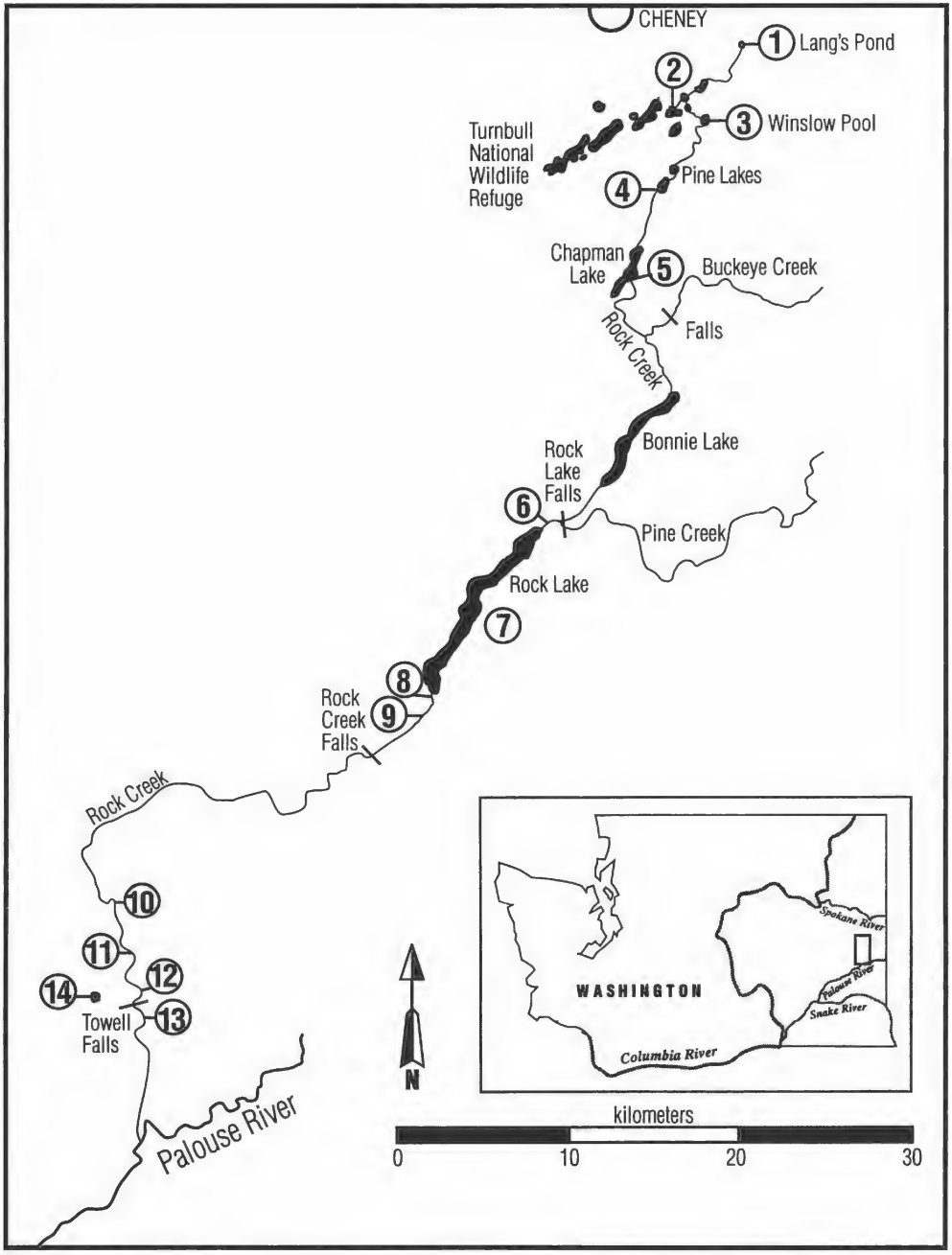


Figure 1. Locations of 14 sites sampled in the Rock Creek drainage, Spokane and Whitman Counties, WA in 1999 and 2000. Refer to Table 1 for latitude and longitude coordinates of each site. Brook sticklebacks were present at sites 1-6 and 14 and absent at sites 7-13.

the taxonomic keys of Scott and Crossman (1973), Becker (1983), and Nelson and Paetz (1992). Voucher specimens were stored in the Eastern Washington University fish collection (Catalog No. EWU 99-001).

In an attempt to discern their origin, pelvic spine length (base to tip) and standard body length (tip of snout to posterior end of caudal peduncle) of 101 brook stickleback were measured to the nearest 0.1 mm using a digital caliper. Previous investigators reported clinal variation in pelvic spine length (Nelson 1969, Andraso and Barron 2002). Specimens from the northwestern portion of their range (Alberta, British Columbia, Northwest Territories) had relatively shorter spines than those from the southeastern portion of their range (Ohio, Michigan, Wisconsin). Several populations from Alberta and the Northwest Territories lacked the pelvic skeleton altogether (Nelson 1969, 1977; Nelson and Atton 1971; Nelson and Paetz 1972; Reist 1981). We plotted pelvic spine length (dependent variable) against standard length (independent variable) of each individual in our sample and compared their distribution to those reported by Nelson (1969) and Andraso and Barron (2002) for brook stickleback populations throughout their natural range.

## Results

In 1999 and 2000, 541 brook stickleback were collected and 4,115 additional specimens were observed at six locations in about 36 km of the Rock Creek watershed in northeastern Washington (Sites 1-6 in Figure 1, Table 1). One additional specimen (at Site 14 in Figure 1, Table 1) was collected from an isolated pond about 24 km downstream from the outlet of Rock Lake in 2000 (Todd Thompson, USDI Bureau of Land Management, Spokane, Washington, personal communication). Brook stickleback were first observed at Sites 1, 5, and 6 in May 1999 and 2–4 in October 1999. They were also collected at Sites 1–5 during the summer of 2000. (Site 6 was not sampled in 2000.)

Mean left pelvic spine length of 101 specimens was 3.0 mm (range 2.1–4.0 mm) (Figure 2). The distribution of pelvic spine lengths in relation to standard body length was more similar to brook stickleback from the southeastern portion of their range than from the northwestern portion of their range (Figure 2).

## Discussion

The present occurrence of brook stickleback in the Rock Creek drainage undoubtedly represents a recent introduction. Five of the 6 sites where stickleback were recovered in 1999 and 2000 (1, 3, 4, 5, 6 in Figure 1) were surveyed between 1980 and 1998, some on multiple occasions, but no stickleback were found. Ludwig and Leitch (1996) and Fuller et al. (1999) noted that stickleback are a common contaminant in bait buckets, which suggests a means of dispersal.

The mean left pelvic spine length in relation to standard body length of our specimens was closer to brook stickleback from the Ohio than those from Alberta (Nelson 1969, Andraso and Barron 2002). Therefore, it appears probable that the brook stickleback in eastern Washington originated from the Midwestern United States.

The point of introduction seems to be near the headwaters of Rock Creek as this was where we observed the greatest abundance. From there, brook stickleback could have rapidly dispersed downstream since six of the seven sites where their presence was recorded were interconnected and the elevation change between them totaled 282 m. A pronounced tendency to disperse downstream has been noted for this species (Lamsa 1963, Manion 1977). In the Rock Creek watershed, dams at Pine and Chapman Lakes and waterfalls act as barriers to block upstream dispersal.

Brook stickleback were found as far downstream as the inlet of Rock Lake. None was collected in the lake (McLellan 2000) or at six sites downstream from the lake. However, the BLM record (Site 14) is from an isolated pond adjacent to Rock Creek in the proximity of the most downstream site we sampled (Site 13). This pond is perched on a basalt terrace 62 m above Rock Creek and has no inlet or outlet, so that it would be impossible for sticklebacks to move from Rock Creek into the pond even during spring freshets.

Cow Creek, a tributary of the Palouse River, and Hangman Creek, a tributary of the Spokane River, were sampled in 1999–2000, but no brook stickleback were found. These were the closest drainages located respectively to the west and east of Rock Creek. These data provide a temporal snapshot for future comparisons.

Introduction of nonidigenous brook stickleback is a matter of concern because they are pugnacious

TABLE 1. Distribution records (1999 and 2000) of brook stickleback in Rock Creek, tributary to the Palouse River, Snake River drainage, Washington.

| Map Location | Location Name | Latitude (°N) Longitude (°W) | No. Collected | No. Observed |
|---|---|---|---|---|
| 1 | Lang's Pond | 047.4654 °N 117.4890 °W | 500 | 2,000 |
| 2 | Reeves Lake | 047.4300 °N 117.5651 °W | 2 | 3–4 |
| 3 | Winslow Pool | 047.4228 °N 117.5374 °W | 2 | 100 |
| 4 | Rock Creek (Pine L. outlet) | 047.4086 °N 117.5340 °W | 6 | 12 |
| 5 | Rock Creek (Chapman L. outlet) | 047.3545 °N 117.5661 °W | 30 | 2,000 |
| 6 | Rock Creek (Rock L. inlet) | 047.2223 °N 117.6331 °W | 1 | 0 |
| 7 | Rock Lake | 047.1866 °N 117.6832 °W | 0 | 0 |
| 8 | Rock Creek (Rock Lake outlet) | 047.1388 °N 117.7242 °W | 0 | 0 |
| 9 | Rock Creek (Hwy. 33) | 047.1240 °N 117.7493 °W | 0 | 0 |
| 10[1] | Rock Creek (BLM 1) | 047.0601 °N 117.9660 °W | 0 | 0 |
| 11[1] | Rock Creek (BLM 2) | 047.0538 °N 117.9713 °W | 0 | 0 |
| 12[1] | Rock Creek (BLM 3) | 046.9837 °N 117.9332 °W | 0 | 0 |
| 13[1] | Rock Creek (BLM 4) | 046.9824 °N 117.9283 °W | 0 | 0 |
| 14[2] | Isolated pond | 046.9942 °N 117.9451 °W | 1 | 0 |

[1] BLM 1-4 refer to four sites sampled on the Escure Ranch, managed by the Bureau of Land Management.

[2] Information from Todd Thompson, USDI, Bureau of Land Management, Spokane, WA. The specimen was collected in an unnamed depressional wetland isolated on a bench above Rock Creek on the Escure Ranch.

and carnivorous. They eat a variety of aquatic invertebrates, especially *Chironomus* larvae and cladocerans (Becker 1983), and fish eggs (Woodling 1985). Therefore, they may compete with or prey upon native species. They are abundant on Turnbull National Wildlife Refuge and could potentially restructure the aquatic communities in refuge ponds and streams.

Given their propensity for downstream displacement, we anticipate that brook stickleback in Rock Creek will eventually spread into the Palouse, Snake, and lower Columbia Rivers. We also predict the imminent spread of Swan River/Flathead Lake populations into the Clark Fork, Pend Oreille and upper Columbia Rivers.

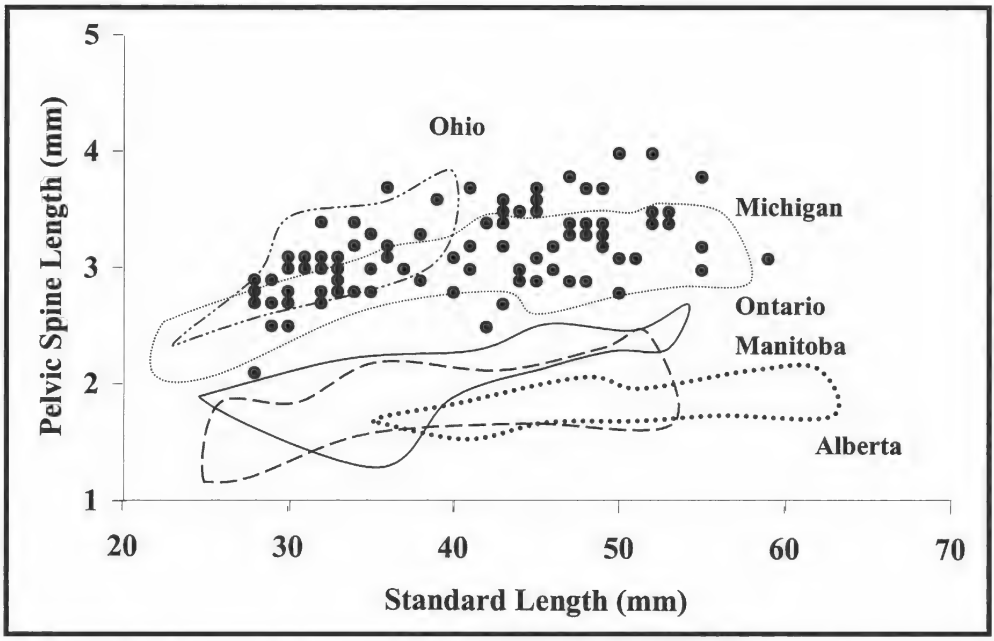


Figure 2. Left pelvic spine length versus standard length of brook stickleback (n = 101) collected from the Rock Creek drainage, Spokane and Whitman Counties, Washington (individual black dots). Shaded areas and enclosed lines indicate the range in variation of pelvic spine length to standard length of brook stickleback collected at five different locations, from southeastern to northwestern portions of their natural range (after Nelson 1969). Pelvic spine lengths of the sticklebacks from eastern Washington were comparable to those found in the Midwest.

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## Literature Cited

Andraso, G. M., and J. N. Barron. 2002. Unusually long spines in brook stickleback (*Culaea inconstans*) from the Mad River Drainage, Ohio. American Midland Naturalist 147:162-169.

Baxter, G. T., and M. D. Stone. 1995. Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Brown, C. J. D. 1971. Fishes of Montana. Big Sky Books, Montana State University, Bozeman, Montana.

Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous Fishes Introduced into Inland Waters of the United States. Special Publication 27. American Fisheries Society, Bethesda, Maryland.

Gilbert, C. H., and B. W. Evermann. 1895. A report upon investigations in the Columbia River Basin, with descriptions of four new species of fish. United States Fish Commission Bulletin 14 (1894):169-202.

Holton, G. D. and H. E. Johnson. 1996. A Field Guide to Montana Fishes, Second Edition. Montana Department of Fish, Wildlife, and Parks, Helena, Montana.

Jordan, D. S., and B. M. Evermann. 1896-1900. The fishes of North and Middle America. A descriptive catalogue

of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Bulletin of the United States National Museum 47(1-4):1-3313 + 392 plates.

Jordan, D. S., B. M. Evermann, and H. W. Clark. 1930. Checklist of the fishes and fish-like vertebrates of North and Middle America north of the boundary of Venezuala and Columbia. Document No.1055. United States Fish Commission. Washington, D.C.

Jordan, D. S., and C. H. Gilbert. 1883. Synopsis of the fishes of North America. Bulletin No. 16 United States National Museum. Washington, D.C.

Lamsa, A. 1963. Downstream movements of brook sticklebacks, *Eucalia inconstans* (Kirkland), in a small southern Ontario stream. Journal of the Fisheries Research Board of Canada 20:587-589.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American Freshwater Fishes. Publication No. 1980-12. North Carolina Biological Survey, Raleigh, North Carolina.

Ludwig, H. R. Jr., and J. A. Leitch. 1996. Interbasin transfer of aquatic biota via angler's bait buckets. Fisheries 21:14-18.

Manion, P. J. 1977. Downstream movement of fish in a tributary of southern Lake Superior. Progressive Fish-Culturist 39:14-16.

McLellan, H. J. 2000. Limnological and fisheries evaluation of Rock Lake, Whitman County, Washington 1999. M.S. Thesis, Eastern Washington University, Cheney, Washington.

McPhail, J. D., and C. C. Lindsey. 1970. Freshwater Fish of Northwestern Canada and Alaska. Bulletin 173. Fisheries Research Board of Canada, Ottowa, Ontario.

Miller, R. R. 1958. Origin and affinities of freshwater fish, fauna, of Western North America. Pages 187-222 *In* C. L. Hubbs (editor), Zoogeography. Publication 51. American Association for the Advancement of Science, Washington, D.C.

Miller, R. R. 1965. Quarternary freshwater fishes of North America. Pages 569-581 *In* H. E. Wright, Jr. and D. G. Frey (editors), The Quaternary of the United States. Princeton University Press, Princeton, New Jersey.

Modde, T., and G. B. Haines. 1996. Brook stickleback (*Culaea inconstans* [Kirtland 1841]), a new addition to the upper Colorado River basin fish fauna. The Great Basin Naturalist 56: 255.

Moyle, P. B. 2002. Inland Fishes of California, Revised and Expanded. University of California Press, Berkley, California.

Mural, R. J. 1973. The Pliocene sticklebacks of Nevada with a partial osteology of the Gasterosteidae. Copeia 1973:721-735.

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Nelson, J. S. 1969. Geographic variation in the brook stickleback, *Culaea inconstans*, and notes on nomenclature and distribution. Journal of the Fisheries Research Board of Canada 26: 2431-2447.

Nelson, J. S. 1977. Evidence of a genetic basis for absence of the pelvic skeleton in brook stickleback, *Culaea inconstans*, and notes on the geographical distribution and origin of the loss. Journal of the Fisheries Research Board of Canada 34:1314-1320.

Nelson, J. S., and F. M. Atton. 1971. Geographic and morphological variation in the presence and absence of the pelvic skeleton in the brook stickleback, *Culaea inconstans* (Kirtland), in Alberta and Saskatchewan. Canadian Journal of Zoology 49: 343-352.

Nelson, J. S., and M. J. Paetz. 1992. The Fishes of Alberta, Second Edition. University of Alberta Press, Edmonton, Alberta.

Reist, J. D. 1981. Variations in frequencies of pelvic phenotypes of brook stickleback in Redwater drainage, Alberta. Canadian Field-Naturalist 95: 178-182.

Schultz, L. P. 1936. Keys to the fishes of Washington, Oregon and closely adjoining regions.. University of Washington Publications in Biology 2:103-228.

Schultz, L. P., and A. P. DeLacy. 1935. Fish of the American Northwest. A catalogue of the fishes of Washington and Oregon, with distributional records and a bibliography. Part 1. Journal of the Pan Pacific Research Institute (Mid-Pacific Magazine) 10:364-380.

Schultz, L. P., and A. P. DeLacy. 1936. Fish of the American Northwest. A catalogue of the fishes of Washington and Oregon, with distributional records and a bibliography. Parts 2—5. Journal of the Pan Pacific Research Institute (Mid-Pacific Magazine) 11: 63-78, 127-142, 211-226, and 275-290.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin 184. Fisheries Research Board of Canada, Ottowa, Ontario.

Simpson, J. L., and R. L. Wallace. 1982. Fishes of Idaho. University of Idaho Press, Moscow, Idaho.

Waite, R. B. 1980. About forty late-glacial Lake Missoula jökulhlaups through southern Washington. Journal of Geology 88: 653-679.

Woodling, J. 1985. Colorado's Little Fish: A Guide to the Minnows and other Lesser Known Fishes of the State of Colorado. Colorado Division of Wildlife, Department of Natural Resources, Denver, Colorado.

Wootton, R. J. 1976. The Biology of Sticklebacks. Academic Press, New York.

Wootton, R. J. 1984. A Functional Biology of Sticklebacks. University of California Press, Berkeley, California.

Wydoski, R., and R. Whitney. 1979. Inland Fishes of Washington. University of Washington Press, Seattle, Washington.

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# Assessing Pacific Lamprey Status in the Columbia River Basin

## Abstract

In the Columbia River drainage, salmonid-based monitoring programs have historically been used to assess status of both adult and juvenile Pacific lamprey. We compared adult lamprey counts at hydropower dams to recent radiotelemetry results and found that the counts underestimated losses between some dams and overestimated passage times through reservoirs. Count data were not correlated with trap captures of adults conducted in the same area and at the same time, likely due to lamprey-specific behaviors that result in inaccurate counts. We recommend maintenance of traditional count protocols, but emphasize the need for continued research to develop an accurate correction factor to apply to these data. Existing salmonid-based sampling for juvenile lamprey is inadequate and we highlight the need for standardized larval lamprey monitoring that provides both abundance and size distributions. Our electrofishing survey for juvenile lamprey indicated that this technique provides critical information on lamprey recruitment and is feasible over large spatial scales.

## Introduction

Protecting native anadromous lamprey populations historically has not been a management priority in the United States (Close et al. 2002a). Even though native lampreys are an important element in river ecosystems (Vladykov 1973), the widely-publicized predation of non-indigenous sea lamprey (*Petromyzon marinus*) on game fishes in the Great Lakes has led to the general perception that all lampreys represent a threat to managed fisheries. However, native lampreys are susceptible to many of the same threats facing recently-listed anadromous species: reduced access to spawning habitat, degradation of spawning and rearing areas, and losses of emigrating juveniles to turbine entrainment, and non-indigenous predators (Renaud 1997). Their protracted residence in freshwater also makes lampreys highly susceptible to pollution. Consequently, the notion that lampreys are invulnerable to extirpation has proved false in some systems (Wallace and Ball 1978, Beamish and Northcote 1989).

Pacific lamprey (*Lampetra tridentata*) occur along the west coast of North America from California to Alaska (Scott and Crossman 1973) and there is concern for their status. Indigenous peoples from the Pacific coast to the interior Columbia River have harvested adult lamprey for subsistence, religious, and medicinal purposes for many generations (Close et al. 2002a). In the Columbia River drainage, adult Pacific lamprey support fisheries that have recently experienced dramatic declines and unprecedented regulation (Kostow 2002). Moreover, concerns about the status of Pacific lamprey resulted in a recent petition to list this species for protection under the Endangered Species Act.

The only historical measure of adult lamprey abundance in the Columbia River is based on visual counts made as lamprey pass through the fishways at hydropower dams (Figure 1) during prespawning migrations (Starke and Dalen 1995). As lamprey move upstream through the fishways, they are crowded into a narrow, lighted channel that is viewed from the side via a glass window. Lamprey counting protocols have been inconsistent. For example, at Bonneville Dam (Figure 1), lamprey were counted in 1938-1969, 1993, for a portion of the migration season in 1997, and for the entire season (15 March- 15 November) since 1998. Lamprey were counted at The Dalles Dam from 1957-1969 and since 1996, and at John Day Dam in 1968-69 and since 1996.

The counting protocols were designed to assess adult salmonid abundance and do not necessarily conform to lamprey migration behavior.

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Figure 1. Study area in the Columbia River drainage. Major hydropower dams are denoted with squares.

Typically, counting is conducted during two consecutive 8-hr shifts from 0500 to 2100 Pacific Daylight Time; however, adult Pacific lamprey are primarily nocturnal (Moser et al. 2002). The erratic swimming behavior of adult lamprey at count windows also make them inherently difficult to count (Starke and Dalen 1995) and can result in multiple counts of each individual (Haro and Kynard 1997, Matter et al. 2000). Seasonal migration patterns can also create profound discrepancies in actual and estimated losses at each reservoir. Beamish (1980) reported that Pacific lamprey overwinter in freshwater and this appears to be the case in the Columbia River, where Pacific lamprey are regularly noted during winter de-watering operations at the hydropower dams (Starke and Dalen 1995). Consequently, lamprey counted in one year may actually have entered the system in the previous year.

Similarly, salmonid-based sampling is an inadequate measure of juvenile lamprey abundance. Juvenile lamprey are collected in traps that target salmonid smolts, but lamprey migrate seaward over a longer time period. Consequently, trap operation schedules would need to be expanded to adequately sample the entire lamprey emigration period (Kostow 2002). In addition, the traps are designed to fish the upper portion of the water column and may not be efficient enough to provide accurate estimates of lamprey abundance. Similarly, the use of fyke and scoop nets to sample salmonids at the turbines and turbine bypasses of hydropower dams could provide useful seasonal or diel trends in relative abundance, but are probably not efficient enough to yield reliable abundance estimates (Long 1968).

The life cycle of the Pacific lamprey is complicated, spanning many different habitats over a broad geographic area. Anadromous adults enter freshwater rivers and can migrate hundreds of kilometers to reach spawning sites in tributary streams. Spawning generally occurs in shallow,

gravel-bottom riffles. Newly hatched ammocoetes (larvae) drift into areas with fine silt or sand and burrow into the sediment where they filter-feed for 4-6 yr (Close et al. 2002a). Consequently, declines in lamprey may be the result of adult losses at sea, inaccurate counts of migrating adults in rivers, or recruitment failure due to loss of spawning or rearing habitats in streams. Thus, methodologies designed to accurately sample all lamprey life stages are needed to assess the status of this species.

The objectives of this study were to: 1) evaluate the accuracy of adult lamprey counts, and 2) assess the feasibility of conducting large-scale electrofishing surveys of ammocoete distribution, relative abundance, and size structure. A radiotelemetry study has been ongoing at the lower Columbia River hydropower dams to assess obstacles to fish passage (Moser et al. 2002). We used radiotelemetry data and trapping in the fishways to make comparisons with lamprey count data. In addition, we sampled for ammocoetes in nine Columbia River tributaries to assess the efficacy of this method relative to salmonid-based assessment of juvenile abundance.

## Study Area

The Columbia River drains over 670,000 km$^2$ and is highly regulated. Starting in the 1930s, with the construction of Bonneville and Rock Island Dams, the main stems of the Columbia and Snake Rivers were nearly completely impounded over the next four decades (Figure 1). Nine dams on the mainstem Columbia River and four dams on the mainstem of the Snake River are equipped with fishways to pass upstream migrants. Pacific lamprey and other anadromous fishes are confined to parts of the drainage below dams without provisions for fish passage: the Columbia River below Chief Joseph Dam and the Snake River below Hells Canyon Dam (Figure 1). We conducted adult lamprey radiotelemetry, and trapping at three lower Columbia River dams: Bonneville, The Dalles, and John Day. We also sampled for larval Pacific lamprey (ammocoetes) in nine Columbia River tributaries: John Day, Middle Fork John Day, North Fork John Day, South Fork John Day , Umatilla, Walla Walla, South Fork Walla Walla, Tucannon, and Grande Ronde (Figure 1). These sub-basins varied widely in size and discharge levels (Table 1), and are areas where lamprey historically occurred.

## Methods

### Trapping and Radiotelemetry

In 1998–2000, we set a trap for lamprey inside a fishway at Bonneville Dam. During nights from May to September we deployed the trap against a wall of the fishway and positioned it at the top of a weir. Lamprey moving over the weir entered the trap and were held in a live box until the trap was fished the following morning. All lamprey were counted, and catch per unit effort (CPUE) was determined by dividing the number of lamprey caught by the number of hours the trap was fished. Yearly CPUE was compared to traditional lamprey counts (visual observations at the counting window) obtained during the same time periods in the same fishway. For 2000, we also compared mean weekly CPUE to mean weekly counts for the same fishway using Spearman's rank correlation procedure (Zar 1999).

In each year we surgically implanted uniquely-coded radio transmitters in large adult lamprey that were collected in the trap. These fish were anaesthetized using either 70 ppm tricaine methane sulfonate (MS222) or 60 ppm clove oil, mea-

TABLE 1. Characteristics of the river basins where juvenile lamprey sampling was conducted in northeastern Oregon and southeastern Washington.

| River Basin | Distance from Pacific Ocean (km) | Area Sampled (rkm) | Elevation (m) | Drainage Area (km$^2$) | Annual Discharge (m$^3$/s) | Precipitation (cm/yr) |
|---|---|---|---|---|---|---|
| John Day | 350 | 64-446 | 61-2,743 | 20,979 | 59.0 | <30-127 |
| Umatilla | 465 | 0-124 | 79-1,768 | 5,931 | 13.0 | 22-140 |
| Walla Walla | 505 | 8-72 | 81-1,800 | 4,553 | 16.1 | 25-100 |
| Tucannon | 623 | 1-57 | 165-1,951 | 1,303 | 4.7 | 25-102 |
| Grande Ronde | 793 | 48-330 | 305-2,438 | 10,360 | 86.8 | 25-152 |

sured (length and girth to the nearest mm) and weighed (nearest g). A radio transmitter representing less than 2% of the lamprey's body weight was then surgically implanted into the body cavity of each fish following the methods of Moser et al. (2002). In all years we used transmitters that were 7.7 g (3.7 g in water), but in 2000 we also used a smaller (4.5 g in air, 2.9 g in water) transmitter. The fish were allowed to recover for 2 hr prior to release below Bonneville Dam.

Movements of radio-tagged lamprey were monitored by an extensive network of fixed-site receivers located on each dam, at the dam tailraces, and at the mouths of major tributaries. Data from fixed-site receivers (fish code, time and date of passage) were downloaded every 1-2 wk and processed following protocols detailed in Moser et al. (2002). In addition, we conducted regular surveys to locate radio-tagged fish using a portable receiver. For each dam, we determined the number of lamprey that exited at the top of the fishway. In 2000, we added additional receivers to document the number of lamprey that passed each counting window at Bonneville Dam and the time of day that lamprey passed by these windows.

The proportion of radio-tagged lamprey lost in each reservoir was computed by subtracting the number of lamprey that passed each successive upriver dam from the number that had passed the previous dam and dividing by the number that passed the previous dam. We computed losses based on visual counts in the same way (U.S. Army Corps of Engineers 1998, 1999, 2000). For each year, we divided the loss obtained from radiotelemetry by the loss obtained from visual counts for two reaches: between Bonneville Dam and The Dalles Dam, and between The Dalles Dam and John Day Dam. We then computed the geometric mean of these annual ratios for each reach. At Bonneville Dam in 2000, we were also able to determine the exact time that lamprey passed the count window. Based on these data, we determined the proportion of lamprey that would have been missed if counts were only conducted during the day (i.e., the number that passed the window at night divided by the total number that passed the window).

### Ammocoete Sampling

In 1999, we sampled for ammocoetes in July-September. We selected sampling sites near the mouth of each river and continued upstream to the headwaters at intervals of 10-16 km, except in the Umatilla River where we sampled every 4 km. The Umatilla River was sampled more intensively because this area was proposed for a lamprey restoration project. Sites were selected based on substrate characteristics, as ammocoetes typically inhabit silty areas (Potter et al. 1986, Young et al. 1990). A 7.5-$m^2$ area was sampled at each site by making two 11.5-min passes with a backpack electrofishing unit. This unit delivered three pulses (125 volts) per second with a 25% duty cycle, and a 3:1 burst pulse train (three pulses on, one pulse off), causing ammocoetes to emerge from the substrate (Weisser and Klar 1990). Thereafter, 30 pulses per second were applied to stun ammocoetes so that they could be dipnetted (Hintz 1993, Weisser 1994). Ammocoetes were then anaesthetized (50 ppm MS222) and measured (nearest mm total length). After ammocoetes recovered, they were returned to the river. Population estimates were determined for each site using methods described in Zippen (1958) and the Capture software program (White et al. 1982). Population estimates were converted into densities (number $m^{-2}$) for each site. Length frequency data were pooled for each river and graphed to assess recent recruitment.

## Results

### Trapping and Radiotelemetry

In the fishway where our trap was deployed at Bonneville Dam, lamprey passage based on count data was 9.4 lamprey $hr^{-1}$ in 1998, 12.7 lamprey $hr^{-1}$ in 1999, and 4.5 lamprey $hr^{-1}$ in 2000. Trap CPUE (lamprey $hr^{-1}$) in those years was 1.0 in 1998, 0.7 in 1999, and 0.3 in 2000. We found no significant correlation between the mean weekly lamprey abundance obtained using the two methods (counts and trap) in 2000.

In 1998, 1999, and 2000, we released 205, 199, and 299 radio-tagged lamprey below Bonneville Dam. In all years the tagged lamprey were greater than 420 g and ranged in length from 60 to 80 cm. Approximately 90% of the fish released below Bonneville Dam in each year resumed upstream migration and approached the dam (Moser et al. 2002). We recaptured two radio-tagged lamprey in our trap in 1999 and four more in 2000. In addition, four radio-tagged lamprey were taken in tribal fisheries. All recaptured individuals were in excellent condition.

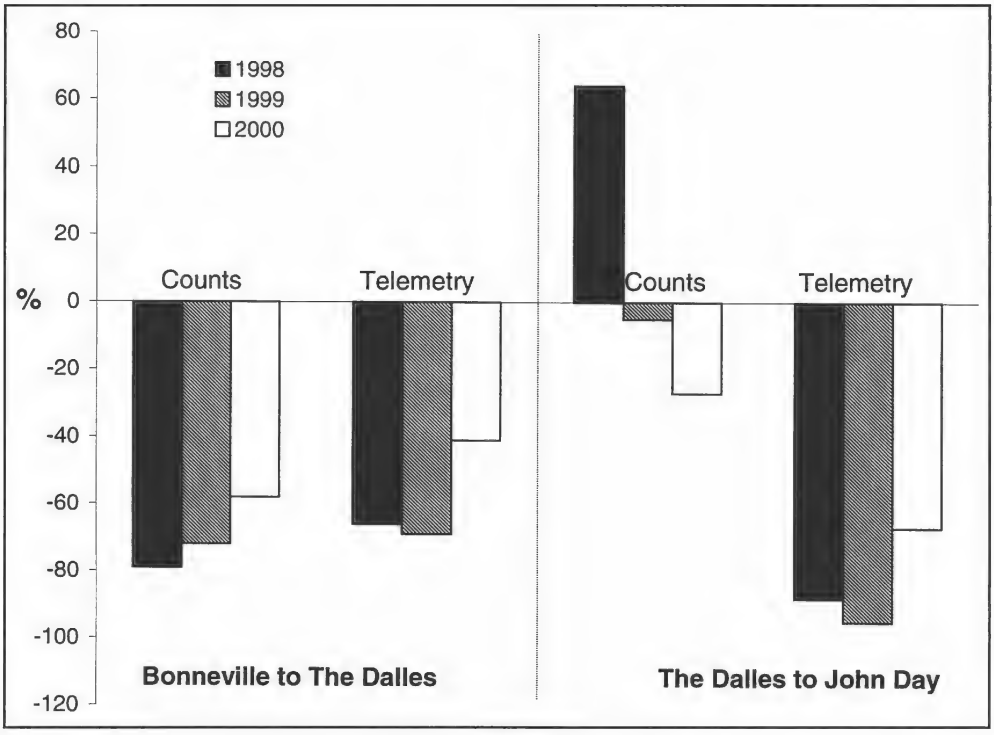


Figure 2. The percentage of adult lamprey lost in each reach (between Bonneville and The Dalles Dams and between The Dalles and John Day Dams) as determined by lamprey counts and radiotelemetry data in 1998-2000.

Radiotelemetry data indicated that lamprey migrated rapidly through the reservoirs and were most active at night. In 1998, mean time to transit the Bonneville Reservoir was 3.5 days and time to transit The Dalles Reservoir was 2.8 days. In contrast, peaks in the counts at Bonneville, The Dalles, and John Day dams indicated that lamprey took 23 days to traverse the Bonneville Reservoir and 35 days to pass through The Dalles Reservoir in 1998 (U.S. Army Corps of Engineers 1998). In 2000, 67% of the lamprey that passed the counting windows at Bonneville Dam would not have been detected because they moved through between 2200 and 0600. In addition, 6% of the radio-tagged lamprey that passed over the dam used routes without count stations (navigation lock and auxiliary water supply channel).

The annual losses we obtained for the area from Bonneville Dam to The Dalles Dam were similar for radiotelemetry vs. count data (geometric mean ratio = 0.83). For this reach the counts yielded slightly higher losses than the telemetry results in all years (Figure 2). However, for the area between The Dalles Dam and John Day Dam, the two methods produced different results. The geometric mean ratio for this reach was 17.98, indicating that the count data underestimated losses relative to radiotelemetry data by a factor of 18, on average. The losses in the reach from The Dalles Dam to John Day Dam based on telemetry were similar to, but consistently higher than, losses based on telemetry for the Bonneville-The Dalles reach (Figure 2).

## Ammocoete Sampling

Ammocoetes were not found in the upper reaches of most tributaries we sampled, nor were they found in any of the Walla Walla River sites (Figure 3). Ammocoete density varied among sites sampled (Table 2). Density was highest in the John Day River and its major tributaries, with over 80 ammocoetes $m^{-2}$ collected at one site in the Middle

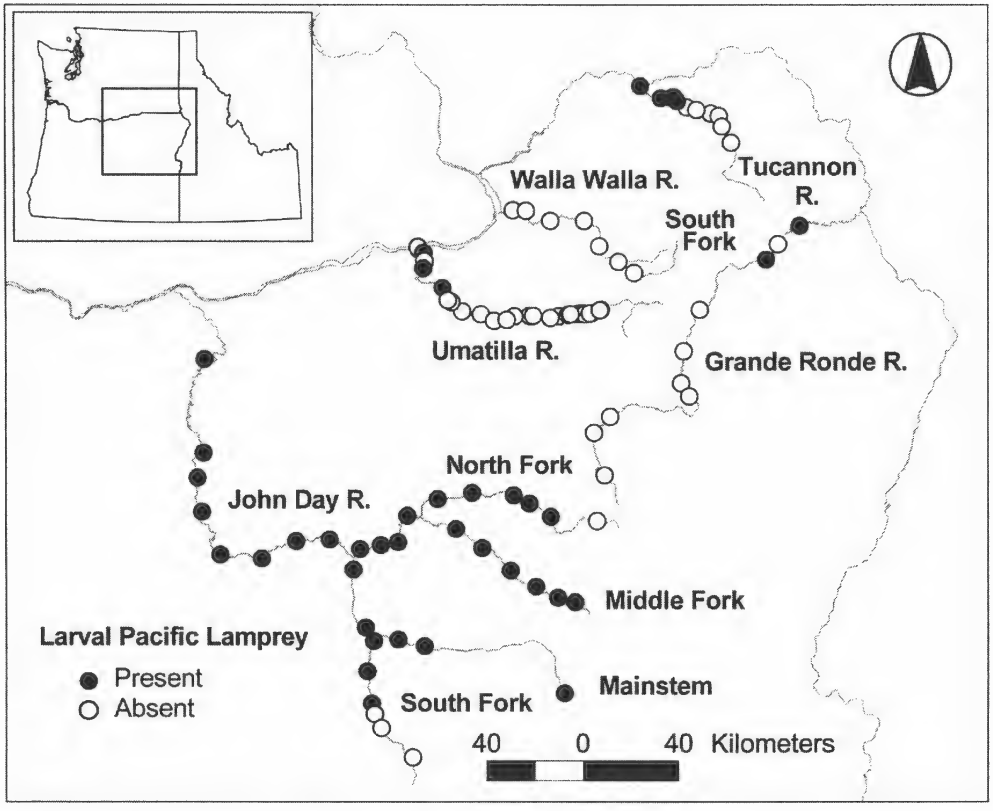


Figure 3. Sampling sites and presence/absence of Pacific lamprey ammocoetes in the mainstem John Day, Middle Fork John Day, North Fork John Day, South Fork John Day, Umatilla, Walla Walla, South Fork Walla Walla, Tucannon, and Grande Ronde Rivers.

Fork. Densities were lowest in the Grande Ronde River, with no more than 2.1 ammocoetes $m^{-2}$ collected at these sites (Table 2). Mean lengths were lowest in the John Day River drainage (except the South Fork), intermediate in the Tucannon, and highest in the Grande Ronde and Umatilla Rivers (Table 2). Examination of length frequency histograms for each sub-basin indicated that sites in the John Day River had larger proportions of lamprey < 60 mm, while the Umatilla, Tucannon, and Grand Ronde collections were dominated by larger year classes (Figure 4).

## Discussion

Our data indicated that lamprey counts at hydropower dams are unreliable and can be misleading. Comparisons between counts at consecutive dams and telemetry results indicated that the counts can produce alarmingly low estimates of losses between dams and can greatly exaggerate the time lamprey required to pass through each reservoir. We found no correlation between trap CPUE and the counts made during the same time periods and in the same fishway at Bonneville Dam. This is not surprising, since more than half of the radio-tagged lamprey passed the counting window during the night, when historically no counts have been taken. We also confirmed that lamprey were able to pass via routes that bypass the counting stations as suggested originally by Starke and Dalen (1995).

Laboratory studies indicate that adult lamprey recover rapidly after transmitter implantation, regaining full swimming capability within 24 hr

TABLE 2. Mean Pacific lamprey ammocoete densities and total lengths in each river and mean river temperatures when lamprey were collected. Range in ( ).

| River | Number of sites | Lamprey density (number m-2) | Lamprey length (mm) | Water temperature (°C) |
|---|---|---|---|---|
| Mainstem John Day | 13 | 12.0 (3.8-36.6) | 56.2 (20-138) | 17.5 (13-20) |
| North Fork John Day | 9 | 26.7 (0-43.3) | 69.6 (12-165) | 21.8 (17-26) |
| Middle Fork John Day | 8 | 32.0 (0-87.1) | 63.1 (18-145) | 19.6 (15-24) |
| South Fork John Day | 6 | 14.2 (0-42.4) | 90.5 (13-166) | 16.0 (12-22) |
| Umatilla | 32 | 0.6 (0-5.2) | 112.1 (29-170) | 21.0 (17-26) |
| Mainstem Walla Walla | 5 | 0 | 0 | 23.8 (19-27) |
| South Fork Walla Walla | 2 | 0 | 0 | 13.5 (10-17) |
| Tucannon | 11 | 5.3 (0-29.8) | 77.8 (24-131) | 13.7 ( 9-17) |
| Grande Ronde | 11 | 0.2 (0-2.1) | 98.3 (75-149) | 15.3 ( 4-23) |

of handling (Close et al. 2003). Consequently, we believe that our radiotelemetry results accurately reflect lamprey travel rates and passage efficiency at dams, and that they reveal problems inherent to traditional adult lamprey assessment. While dam counts are clearly problematic, they have been taken in a fairly consistent manner and represent the only historical measure of relative abundance. Continued radiotelemetry or passive integrated transponder (PIT) technology should be used to develop an accurate correction factor to be applied to the count data.

In 2000, a surprisingly large number of radiotagged lamprey were recaptured in our trap and in tribal fisheries, despite relatively low fishing effort. This suggests that a mark and recapture program in tributaries may be a feasible alternative for obtaining absolute abundance estimates of adult lamprey. Tagging studies have historically been used to assess homing (Tuunainen et al. 1980, Bergstedt and Seelye 1995); however, recent tag/recapture studies have produced reliable estimates of adult sea lamprey abundance in tributaries of the Great Lakes (Kasia Mullett, U. S. Fish and Wildlife Service, Marquette, Michigan, personal communication). Tag/recapture studies and counts of Pacific lamprey nests (redds) are being conducted in Cedar Creek, a small tributary of the Columbia River (Stone et al. 2001). While redd counts can provide valuable information on spatial and temporal patterns of lamprey spawning, it is unclear that they can document adult abundance because lamprey may dig more than one redd. Redd sampling in the Umatilla River also indicated that many lamprey redds did not contain viable eggs.

Juvenile lamprey abundance was highly variable (0 – 87 ammocoetes $m^{-2}$) within and among the rivers we sampled, in spite of our efforts to target primary ammocoete habitat. This result highlights the need to couple habitat delineation with ammocoete sampling to allow adequate stratified sampling at appropriate scales (Pajos and Weise 1994). The aim of our sampling was to provide data on lamprey occurrence over a broad spatial scale. To obtain reliable estimates of relative abundance, higher resolution sampling and detailed habitat mapping are needed (Christian Torgerson, Oregon State University, Corvallis Oregon, personal communication). In addition, standardized electrofishing methodology is critical to ensure that capture efficiency is comparable among sampling programs (Pajos and Weise 1994).

Although tedious and labor-intensive, measuring juvenile lamprey provides important information on individual cohorts. The absence of ammocoetes in the upper reaches of most rivers we sampled indicated that there has been complete recruitment failure in these areas in recent years. We speculate that this is largely due to the presence of large hydropower dams and low-head diversion dams that restrict access of adults to spawning areas that are farthest upstream. The truncated size distributions of ammocoetes collected in the Umatilla and Grande Ronde Rivers further suggest that there has not been recent spawning success in these areas. Unfortunately, reliable ageing techniques have not been developed for lamprey (Barker et al. 1997). Until reliable ageing methods are worked out, we recommend that size data be collected during juvenile lamprey sampling programs.

Current assessment methods for Pacific lamprey in the Columbia River drainage are inadequate. Our data also indicated that lamprey have experienced

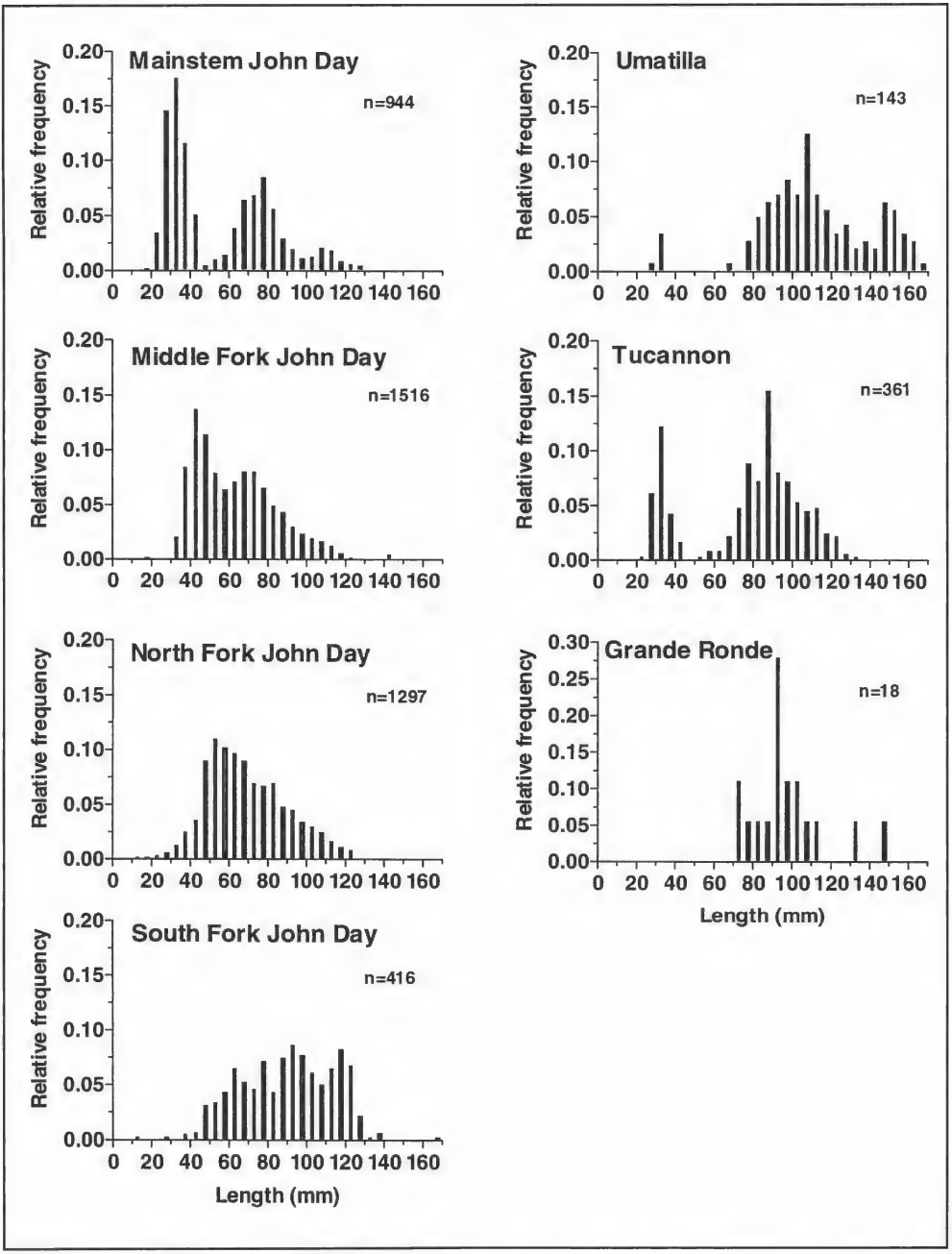


Figure 4. Distribution of larval lamprey lengths (mm) observed in the Mainstem John Day, Middle Fork John Day, North Fork John Day, South Fork John Day, Umatilla, Tucannon, and Grande Ronde Rivers.

poor recruitment in the uppermost reaches of rivers where this fish has historically been captured. These data highlight the need for comprehensive status assessment of Pacific lamprey. We recommend the use of standardized larval sampling, maintenance of historical measures of adult lamprey passage, and the use of other technologies to obtain more reliable estimates of adult abundance. Most importantly, we underscore the need to heighten awareness of threats to native lampreys and to promote collection of lamprey data in existing surveys. Conservation of lampreys can only proceed by changing the established perceptions that these fishes are invulnerable to extirpation and represent a threat to more desirable species.

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## Literature Cited

Barker, L. A., B. J. Morrison, B. J. Wicks, and F. W. H. Beamish. 1997. Age discrimination and statolith diversity in sea lamprey from streams with varying alkalinity. Transactions of the American Fisheries Society 126:1021-1026.

Beamish, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific Coast of Canada. Canadian Journal of Fisheries and Aquatic Sciences 37:1906-1923.

Beamish, R. J., and T. G. Northcote. 1989. Extinction of a population of anadromous parasitic lamprey, *Lampetra tridentata*, upstream of an impassable dam. Canadian Journal of Fisheries and Aquatic Sciences 46:420-425.

Bergstedt, R. A., and J. G. Seelye. 1995. Evidence for lack of homing in sea lamprey. Transactions of the American Fisheries Society 124:235-239.

Close, D. A., M. S. Fitzpatrick, and H. W. Li. 2002a. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. Fisheries 27:19-25.

Close, D. A., M. S. Fitzpatrick, C. M. Lorion, H. W. Li, C. B. Schreck. 2003. Effects of intraperitoneally implanted radio transmitters on the swimming performance and physiology of Pacific lamprey. North American Journal of Fisheries Management (in press).

Haro, A., and B. Kynard. 1997. Video evaluation of passage efficiency of American shad and sea lamprey in a modified Ice Harbor fishway. North American Journal of Fisheries Management 17:981-987.

Hintz, A .K. 1993. Electrofishing burrowed larval sea lamprey (*Petromyzon marinus*), the effect of slow pulsed direct current variables on emergence at varying water temperatures. M.S. Thesis, Central Michigan University, Mount Pleasant, Michigan.

Long, C. W. 1968. Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. Fishery Bulletin 66:599-609.

Kostow, K. 2002. Oregon lampreys: Natural history, status, and analysis of management issues. Oregon Department of Fish and Wildlife, Portland, Oregon.

Matter, A. L., J. J. Vella, and L. C. Stuehrenberg. 2000. Migration passage patterns of Pacific lamprey at Bonneville Dam, 1996-1998. Pages 278-285 *In* J. H. Eiler, D. J. Alcorn, and M. R. Neuman (editors), Biotelemetry 15, International Society on Biotelemetry, Wageningen, The Netherlands.

Moser, M. L., A. L. Matter, L. C. Stuehrenberg, and T. C. Bjornn. 2002. Use of an extensive radio receiver network to document Pacific lamprey (*Lampetra tridentata*) entrance efficiency at fishways in the lower Columbia River. Hydrobiologia 483:45-53.

Pajos, T. A., and J. G. Weise. 1994. Estimating populations of larval sea lamprey with electrofishing sampling methods. North American Journal of Fisheries Management 14:580-587.

Potter, I. C., R. W. Hilliard, J. S. Bradley, and R. J. McKay. 1986. The influence of environmental variables on the density of larval lamprey in different seasons. Oikos 70:433-440.

Renaud, C. B. 1997. Conservation status of Northern Hemisphere lamprey (Petromyzontidae). Journal of Applied Ichthyology 13:143-148.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa.

Starke, G. M., and J. T. Dalen. 1995. Pacific lamprey (*Lampetra tridentata*) passage patterns past Bonneville Dam and incidental observations of lamprey at the Portland

District Columbia River dams in 1993. Unpublished report on file at U.S. Army Corps of Engineers, Bonneville Lock and Dam, Fish Field Unit, CENPP-OP-PF, Cascade Locks, Oregon.

Stone, J., T. Sundlov, S. Barndt, and T. Coley. 2001. Evaluate habitat use and population dynamics of lampreys in Cedar Creek. Unpublished annual report to Bonneville Power Administration, U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, Vancouver, Washington.

Tuunainen, P., E. Ikonen, and H. Auvinen. 1980. Lamprey and lamprey fisheries in Finland. Canadian Journal of Fisheries and Aquatic Sciences 37:1953-1959.

U.S. Army Corps of Engineers. 1998. Annual Fish Passage Report: Columbia and Snake Rivers for Salmon, Steelhead, and Shad. North Pacific Division, U.S. Army Corps of Engineers, Portland, Oregon.

U.S. Army Corps of Engineers. 1999. Annual Fish Passage Report: Columbia and Snake Rivers for Salmon, Steelhead, and Shad. North Pacific Division, U.S. Army Corps of Engineers, Portland, Oregon.

U.S. Army Corps of Engineers. 2000. Annual Fish Passage Report: Columbia and Snake Rivers for Salmon, Steelhead, and Shad. North Pacific Division, U.S. Army Corps of Engineers, Portland, Oregon.

Vladykov, V. D. 1973. North American nonparasitic lamprey of the family Petromyzontidae must be protected. Canadian Field-Naturalist 87:235-239.

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Wallace, R. L., and K. W. Ball. 1978. Landlocked parasitic Pacific lamprey in Dworshak Reservoir, Idaho. Copeia 1978:545-46.

Weisser, J. W. 1994. Response of larval sea lamprey *(Petromyzon marinus)* to electrical stimulus. M.S. Thesis, Northern Michigan University, Marquette, Michigan.

Weisser, J. W., and G. T. Klar. 1990. Electric fishing for sea lamprey *(Petromyzon marinus)* in the Great Lakes region of North America. Pages 59-64 *In* I. G. Cowx (editor), Developments in Electric Fishing, Cambridge University Press, Cambridge, U.K.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Publication 1982-576-020/141. U. S. Government Printing Office, Washington, D.C.

Young, R. J., J. R. M. Kelso, and J. G. Weise. 1990. Occurrence, relative abundance, and size of landlocked sea lamprey *(Petromyzon marinus)* ammocoetes in relation to stream characteristics in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 47:1773-1778.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall. Englewood Cliffs, New Jersey.

Zippin, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22:82-90.

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# A Comparison of Bat Activity at Low and High Elevations in the Black Hills of Western Washington

## Abstract

We examined the differences in activity patterns and community structure of bats between low (< 150 m) and high (≥ 575 m) elevation sites in two habitats of the Capitol State Forest, Washington. Total bat activity averaged four times higher at low elevation sites than at high elevation sites. Feeding activity was almost 20 times higher at low elevation sites. However, the non-myotis group had similar activity levels at high and low elevation, whereas myotis group activity decreased at higher elevations. Different levels of activity between elevations could be the result of differences in insect availability, climatic conditions, and morphology of the bat species.

## Introduction

That fewer bats occupy high elevation regions compared to lowland regions is a familiar pattern to many mammalogists. Changes in elevation are ecologically similar to changes in latitude. However, unlike latitudinal patterns in bat diversity that have received considerable attention (Findley and Wilson 1983, Willig and Selcer 1989), elevational gradients have seldom been investigated. An exception to this is a study that examined the variation in bat community attributes along an elevational gradient in the central Andes of Peru (Graham 1983). Graham found that of the 101 species distributed along this gradient, 82 occurred below 400 m and only 10 above 3200 m. He hypothesized that the reduction in insectivorous bat species in the highlands might be explained by a reduction in roost site availability, temperature, or insect abundance.

In the Pacific Northwest, Thomas and West (1991) found no breeding individuals above 300 m in the western Washington Cascade Range. Others have reported decreases in relative abundance of reproductive individuals at high elevations in south-central British Columbia (Fenton et al. 1980) and the Black Hills of South Dakota (Cryan et al. 2000). Moreover, foraging activity is greater at low elevation sites than at high elevation sites in southern British Columbia (Grindal and Brigham 1999). The authors suggested that foraging opportunities limit bat use of high elevational forests because the cooler conditions may decrease activity of their insect prey while imposing greater thermoregulatory costs.

Apart from the work by Thomas and West (1991), there is no information available concerning elevational patterns in bat activity and species composition in western Washington. The objective of this study was to compare levels of bat activity, weather conditions, and insect abundance between low (< 150 m) and high (≥ 575 m) elevations in two habitats of a Pacific Northwest forest ecosystem.

## Methods

The study was conducted at Capitol State Forest (46°57 N, 123°10 W) and Lower Chehalis State Forest (46°83 N, 123°38 W) located in the Black Hills ~24 km west of Olympia, Washington. The forests include more than 34,000 ha of multiple use areas under the stewardship of the Washington State Department of Natural Resources. The forests are a mix of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*),

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western red cedar *(Thuja plicata)*, red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). Three pronounced peaks that reach > 800 m in elevation dominate the study area, but the terrain generally lies at < 200 m. Due to prevailing westerly winds and close proximity to the ocean, the area is characterized by rapidly changing weather often resulting in wet conditions.

During summer 1995, activity was monitored at eight sites located within two elevational zones. For purposes of our study, low elevation sites were < 150 m and high elevation sites were ≥ 575 m. The high elevation sites were centered on Rock Candy Mountain (718 m), Larch Mountain (810 m), and Capitol Peak (810 m). Two ponds and two clearings were selected for monitoring bat activity within each elevational zone.

Bats were surveyed using remotely deployed ultrasonic detectors (Anabat II bat detectors and delay switches) coupled with tape recorders to record echolocation calls of bats. Two detectors were operated simultaneously, one at low elevation and one at high elevation within the same habitat. These were left in place for two nights before being moved to the next pair of sites. Pond detector stations were located ~1 m from the water's edge facing the pond center. Detector stations located in clearings were placed on stumps ~1 m high and also directed toward the site center. These habitats were sampled from mid-June through late September.

For purposes of this study, a detection was operationally defined as two or more consecutive pulses recorded as a bat flies through the airspace sampled by the microphone. Commuting activity was identified as a steady series of echolocation calls and foraging activity was identified by a distinctive train of pulses with an increasing repetition rate (Griffin 1958). Activity was indexed as the mean number of detections per night within each site. Because bat activity was concentrated within the first 4 hr after sunset, differences in total night length over the sampling period were not considered influential on nightly detection totals.

Recorded detections were analyzed at two levels. First, detections were summed regardless of species to determine the general distribution of detections among sites. Second, detections were grouped into myotis and non-myotis bats based on call characteristics using zero-crossing analysis and signal processing software (Anabat V). The myotis group comprised California myotis (*Myotis californicus*), long-eared myotis (*M. evotis*), little brown myotis (*M. lucifugus*), fringed myotis (*M. thysanodes*), long-legged myotis ( *M. volans*), and Yuma myotis (*M. yumanensis*). The non-myotis group comprised big brown bats (*Eptesicus fuscus*), silver-haired bats (*Lasionycteris noctivagans*), hoary bats (*Lasiurus cinereus*), and Townsend's big eared bats (*Corynorhynus townsendii*). Members of the myotis group are typically small, agile bats that have high frequency, short duration calls. The larger bats of the non-myotis group are characterized as faster, less maneuverable species with low frequency, long duration calls. Separation between these groups, although coarse, does provide insight into ecological differences based on morphology and echolocation call design.

Temperature and wind were monitored at the two elevations using mobile weather stations. Sensors were mounted 1 m above the ground and measurements for each variable were recorded hourly. Throughout the summer, one high and one low elevation site of the same habitat (i.e., pond or clearing) was monitored simultaneously for ~1 wk then rotated to the next pair of sites. Nightly temperature (°C) and wind speed (km/hr) were then averaged over all visits within each elevational zone.

We used a sticky trap method and a headlight transect method to provide relative measures of insect abundance at low and high elevations. The sticky trap method consisted of a plastic film wrapped around two tin coffee cans attached end to end. Each set of cans was fastened to a metal rod 2 m above ground level or placed on an inner tube and floated over water. A thin coat of adhesive was applied to the outer surface of the cylinder. Insects landing on the cylinder adhered to the sheet.

A high and low elevation site was sampled concurrently with four sticky traps each. Insects were collected from traps over two consecutive days on eight occasions in each habitat/elevation combination. Insects were classified into large (> 5 mm in length) and small (≤ 5 mm in length) size categories. Ideally, traps would have been cleared simultaneously after every nightly sampling period. Logistical constraints, however, required us to clear traps opportunistically when we visited sites.

Headlight transects were also conducted along two parallel roads located at high and low elevations to sample moth density. The 3.2 km transects were driven ~15-20 min after dusk during which time all moths spotted within the headlights were counted. Both low and high elevation counts were performed weekly.

Because bat activity and insect abundance closely resembled a Poisson distribution, an analysis of deviance (ANODEV) with a log-linear model and Poisson error (GLIM 4.0) (Francis et al. 1993) was used to examine the effect of elevation and habitat on average bat activity and insect abundance (McCullagh and Nelder 1989). The models were overdispersed so that the F-statistic was used to determine significance (Crawley 1993). T-tests were used to compare differences in nightly temperature and wind speed at the two elevations and a paired t-test was used to evaluate differences in moth abundance (SYSTAT 7.0, Wilkinson 1996). Significance was set at $P = 0.05$. We also report mean ± SE.

## Results

We recorded 3206 detections over 122 detector nights. Of the total detections, 2559 were classified in the myotis group, 642 were classified in the non-myotis group, and 5 were unidentifiable. Myotis group activity was significantly associated with habitat and elevation (Table 1), with the highest activity rates found at low elevation ponds (Figure 1). No significant patterns in non-myotis group activity were detected (Table 1, Figure 1).

Nightly activity patterns differed between elevations (Figure 2). At low elevations, a distinct peak in activity occurred between 2000 and 2300 hr. However, at high elevations the activity was much more protracted throughout the night with no obvious peaks in detection rates.

TABLE 1. Analysis of deviance for mean number of bat detections per night with elevation and habitat type.

| Source | df | Deviance | F | *P* |
|---|---|---|---|---|
| Myotis group | | | | |
| Elevation | 1 | 1108.0 | 14.11 | 0.020 |
| Habitat | 1 | 1951.0 | 24.84 | 0.008 |
| Elevation×Habitat | 1 | 9.111 | 0.12 | 0.751 |
| Residual | 4 | 314.21 | | |
| Non-Myotis group | | | | |
| Elevation | 1 | 12.56 | 0.14 | 0.732 |
| Habitat | 1 | 230.0 | 2.47 | 0.191 |
| Elevation×Habitat | 1 | 25.94 | 0.28 | 0.625 |
| Residual | 4 | 372.07 | | |

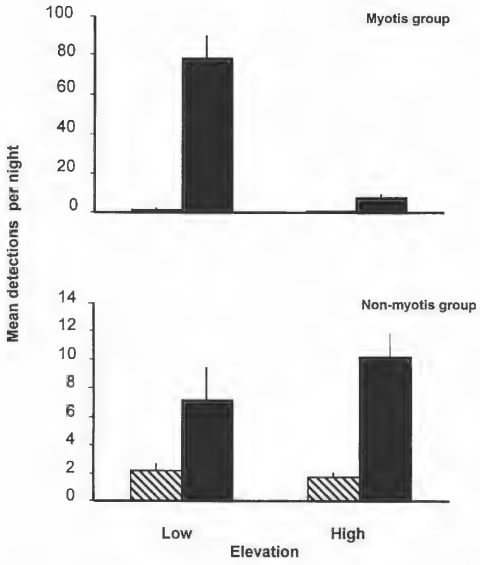


Figure 1. Mean detections per night of myotis and non-myotis bats. Solid bars represent ponds and hatched bars represent clearings. Error bars show standard error.

Of the 3206 detections, 195 were identified as feeding activity. Low ponds had the highest number of feeding attempts per night ($\bar{x} = 6.1 \pm 7.82$). All other sites had less than one feeding attempt recorded per night.

Of the 4676 insects captured using sticky traps, 4125 were small and 551 were large. Overall, insect abundance was greatest at low elevation sites (Figure 3). Small insects were most common in low elevation clearings and no significant difference was detected between high and low elevation ponds (Table 2, Figure 3). We detected no trends in the abundance of large insects caught in sticky traps. Significantly more moths were encountered at low elevation sites ($\bar{x} = 11.30$) than high elevations sites ($\bar{x} = 6.63$; $P < 0.001$) during headlight transects.

On average, nights at high elevation were 2.3°C cooler ($\bar{x} = 11.70$°C) than at low elevations ($\bar{x} =$

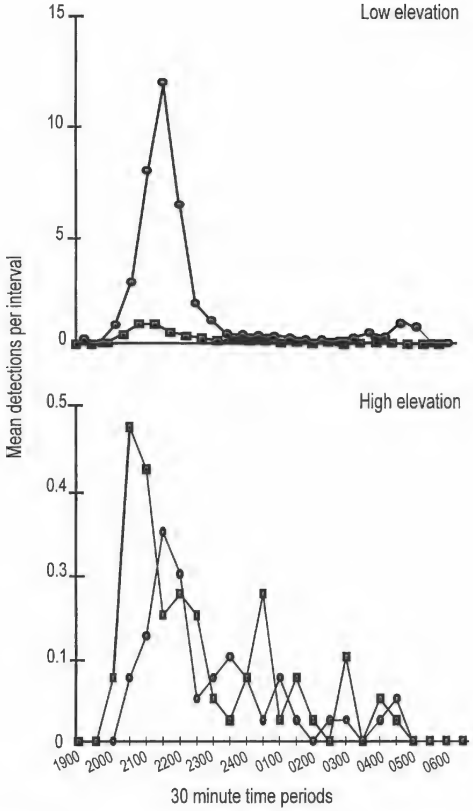


Figure 2. Mean detections per time interval of myotis ( • ) and non-myotis bats (▪) at low elevation and high elevation. Intervals are 30 min time periods beginning at 1900 hr and ending at 0700 hr.

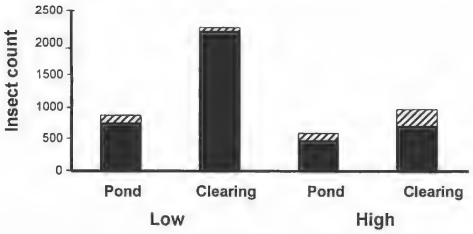


Figure 3. Total number of insects captured by habitat and elevation. Hatched bars represent large insects (>5 mm) and black bars represent small insects (≤ 5 mm).

14.00°C, $P < 0.001$). Similarly, windspeed was 2.9 km/hr greater in the highlands ($\bar{x} = 5.71$ km/hr) than in the lowlands ($\bar{x} = 2.86$ km/hr, $P < 0.001$).

TABLE 2. Analysis of deviance for mean number of insects captured per trapping interval with elevation and habitat type.

| Source | df | Deviance | F | *P* |
|---|---|---|---|---|
| Small (<5mm) | | | | |
| Elevation | 1 | 875.9 | 73.36 | 0.001 |
| Habitat | 1 | 517.7 | 43.36 | 0.003 |
| Elevation×Habitat | 1 | 149.2 | 12.50 | 0.024 |
| Residual | 4 | 47.758 | | |
| Large (>5mm) | | | | |
| Elevation | 1 | 28.80 | 1.29 | 0.320 |
| Habitat | 1 | 6.928 | 0.31 | 0.608 |
| Elevation×Habitat | 1 | 43.45 | 1.94 | 0.236 |
| Residual | 4 | 89.503 | | |

## Discussion

We found distinct differences in bat activity between elevations and habitats for the myotis group, but not for the non-myotis group. Activity levels of the myotis group were significantly greater at low elevation sites; however, no elevational patterns in non-myotis activity were detected (Figure 1). These elevational differences in activity could be the result of climatic conditions, insect availability or morphological differences between myotis and non-myotis bats.

Cooler and windier nights, such as in the highlands, tend to suppress flight activity of bats (Anthony et al. 1981, O'Farrell 1967, Stebbings 1968) by imposing thermoregulatory stress and by reducing the activity of their insect prey. Barclay (1991) and Cryan et al. (2000) suggest that females move from cool hibernation sites in the mountains to warm maternity colonies at lower elevations where ambient temperature and presumably insect abundance is higher. The absence of reproductive individuals could, therefore, result in lower total bat activity at high elevation sites.

Differences in morphology may also influence the elevational distribution of bats. Because the cost of flight increases with decreasing size, de Jong (1994) hypothesized that smaller bats with slower flight would be restricted from using high elevation habitats where insect abundance was low and long-distance foraging flights were required to find enough food. Such long distance flights would be too energetically expensive for small species but not for larger species. This greater mobility may allow larger-bodied non-myotis bats to use a range of elevations for foraging depending on nightly weather conditions or other factors.

Differences in prey detection capabilities also could influence the activity patterns of bats at different elevations. It has been suggested that large bats are restricted to relatively large prey because their lower frequency calls make it difficult to detect small insects (Barclay and Brigham 1991). The lack of elevational trends in non-myotis group activity (Figure 1) and large insect abundance (Figure 3) is consistent with the hypothesis that larger bat species cover a range of elevations in search of larger insects. However, our study cannot link bat distribution to feeding preferences.

The relationship between bat activity and elevation is complex due to its multi-factorial nature, nonetheless, in this study elevation was associated with bat activity and distribution. Further investigations of species-specific responses to elevation are needed especially in light of the predominance of high elevation reserves in the Northwest Forest Plan (Forest Ecosystem Management Assessment Team 1993). Given this and other studies showing a decrease in bat activity (Grindall and Brigham 1999) or relative abundance (Fenton et al. 1980, Thomas and West 1991, Cryan et al. 2000) with elevation, the effectiveness of these reserves for some bats, especially myotis species, requires further verification.

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## Literature Cited

Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. Oecologia 51:151-156.

Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. Journal of Animal Ecology 60:165-178.

Barclay, R. M. R., and R. M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? American Naturalist 137:693-703.

Crawley, M. J. 1993. Glim for Ecologists. Blackwell Scientific Publications, Boston, Massachusetts.

Cryan, P. M., M. A. Bogan, and J. S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. Journal of Mammalogy, 81:719-725.

de Jong, J. 1994. Distribution patterns and habitat use by bats in relation to landscape heterogeneity, and consequences for conservation. Ph.D. Dissertation, University of Agricultural Sciences, Uppsala, Sweden.

Fenton, M. B., C. G. Van Zyll de Jong, G. P. Bell, D. B. Campbell, and M. Laplante. 1980. Distribution, parturition dates and feeding of bats in south-central British Columbia. Canadian Field Naturalist 94:416-420.

Findley, J. S., and D. E. Wilson. 1983. Are bats rare in tropical Africa? BioTropica 15:299-303.

Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team. 1993-793-071. U.S. Government Printing Office, Washington, D.C.

Francis B., M. Green, and C. Payne (editors). 1993. GLIM 4: the statistical system for generalized linear interactive modelling. Oxford University Press, New York.

Graham, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. Journal of Mammalogy 64:559-571.

Griffin, D. R. 1958. Listening in the Dark: The Acoustic Orientation of Bats and Man. Yale University Press, New Haven, Connecticut.

Grindal, S. D., and R. M. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. EcoScience 6:25-34.

McCullagh, P., and J. A. Nelder. 1989. Generalized Linear Models. Chapman and Hall, London, U.K.

O'Farrell, M. J. 1967. Fall and winter bat activity at a desert spring in southern Nevada. Southwestern Naturalist 12:163-171.

Stebbings, R. E. 1968. Measurements, composition and behavior of a large colony of the bat *Pipistrellus pipistrellus*. Journal of Zoology 156:15-33.

Thomas, D. W., and S. D. West. 1991. Forest age associations of bats in the southern Washington Cascade and Oregon Coast Ranges. Pages 295-301 *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (technical coordinators), Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.

Wilkinson, L. 1996. SYSTAT 7.0 for Windows. SPSS Inc., Chicago, Illinois.

Willig, M. R., and K. W. Selcer. 1989. Bat species density gradients in the New World: a statistical assessment. Journal of Biogeography 16:189-195.

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# Translocating Roosevelt Elk for Site Specific Herd Augmentation: Two Case Studies

## Abstract

The state of Washington and four Native American tribes on the east Olympic Peninsula cooperatively conducted single translocations of 17 Roosevelt elk into the Dosewallips drainage in 1995 and 24 elk into the Skokomish drainage in 1997, in attempts to augment the small resident herds. Three of the elk translocated into the Dosewallips and 12 of those translocated into the Skokomish were fitted with radio-collars and monitored for 3 yr post-translocation for survival and movement. Survival of elk translocated into the Dosewallips could not be calculated due to insufficient sample size, but survival of elk translocated into the Skokomish averaged 0.65 ± 0.04 for the first 2 yr and was 0.80 the third year post-translocation. This compares with survival of 0.91 ± 0.02 for 43 resident elk from six herds in the east Olympics from 1993-2000. Of the elk translocated into the Dosewallips, 41% remained with the resident herd for at least 1 yr, while only 4% of the translocated elk remained with the Skokomish herd for 1 yr. All radio-collared elk translocated into the Skokomish dispersed singly or in small groups an average of 20 km in the general direction of the source herd. The population in the Dosewallips herd increased from 26 to 46 within 1 yr of the translocation, and has remained stable at the higher level. The Skokomish herd increased from 17 to 25 after the translocation, but subsequently declined to 15.

## Introduction

Translocation is a commonly used method for reestablishing wildlife populations. Many species, including elk (*Cervus elaphus*) (Harper 1987), wolves (*Canis lupus*) (Bangs and Fritts 1996), and cougar (*Felis concolor*) (Ruth et al. 1998) have been successfully reintroduced to their former range via translocation. Over 1,200 Roosevelt (*C. e. roosevelti)* and Rocky Mountain elk (*C. e. nelsoni*) have been released at more than 50 sites throughout the Cascade Mountains in Washington and Oregon since 1947, primarily to reestablish herds that were eliminated by overhunting (Harper 1987). Data on number of elk released at a time, survival, or movement after translocation are not available from these early translocations. The goal of most translocations has been to reestablish extirpated herds or to supplement populations at a Game Management Unit (GMU) or larger scale. We know of no reported studies in which translocation was used specifically to supplement a small existing elk herd in a single drainage within a GMU.

Elk dispersing from small, reintroduced populations have been reported to be subject to high rates of mortality (Geist 1982, Witmer 1990). Survival of translocated elk in Oregon was 0.77, compared with resident elk survival of 0.89 in Oregon from 1984-1990, 0.89 in Idaho from 1986-1991, and 0.86 in Washington from 1989-1993 (Unsworth et al. 1993, Stussy et al. 1994, Smith et al. 1994). Successful population augmentation, especially at the small river drainage scale, depends not only on survival of translocated individuals, but also on their developing site fidelity. Few studies, however, have addressed movement of translocated elk.

Roosevelt elk within the Dosewallips River drainage on the east Olympic Peninsula, Washington (Figure 1), declined from an estimated 150 animals in the 1930s to 47 elk in 1985, and 24 animals by 1990 (Schwartz and Mitchell 1945, Schroer 1986). Elk population declines are often related to changes in habitat. However, elk in the Dosewallips drainage spent most of their time foraging in agricultural fields and riparian areas, which have not changed in size since 1985. Despite the availability of high quality forage in the Dosewallips, the population declined. State and

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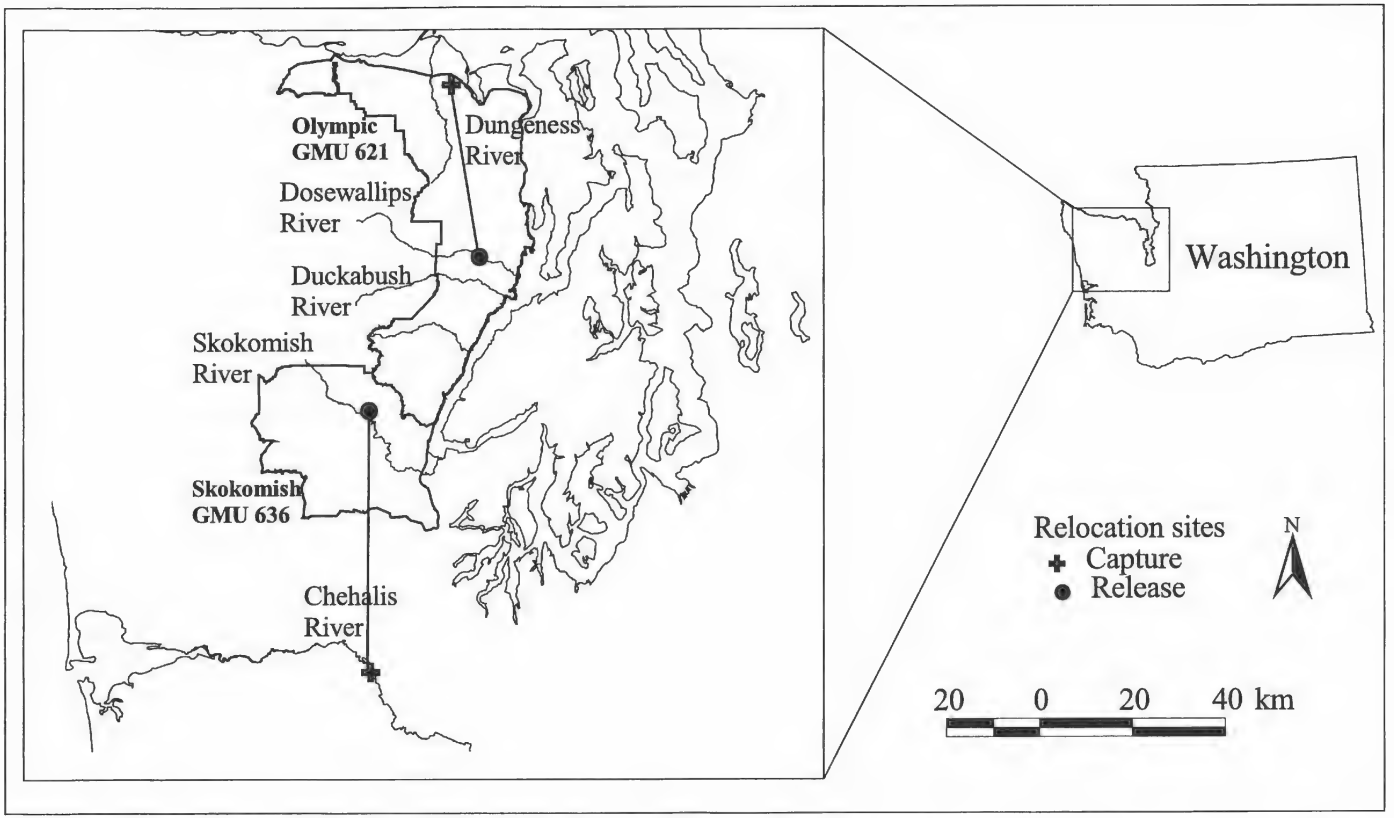


Figure 1. Capture and release sites for Roosevelt elk translocated to the Dosewallips drainage (Olympic GMU 621) in 1995 and to the Skokomish drainage (Skokomish GMU 636) in 1997, Olympic Peninsula, Washington.

tribal harvest data indicate that cow harvest in the 1980s was sufficient to cause the decline since 1985. The cause of the population decline from the 1930-1985 is unknown, but may be related to timber harvest patterns, the increase in human population in the drainage, and elk harvest.

To facilitate population recovery, the four Point No Point Treaty Council (PNPTC) tribes, consisting of the Skokomish, Port Gamble S'Klallam, Jamestown S'Klallam and Lower Elwha Klallam tribes, closed tribal hunting on the Dosewallips herd in 1990. The elk population remained unchanged however, and in 1993 the Washington State Department of Fish and Wildlife (WDFW) and the PNPTC tribes closed the entire Olympic GMU to elk hunting. The Dosewallips herd remained static at about 24 animals despite the hunting ban.

A similar situation occurred in the Skokomish GMU in the southeast Olympics. The herd in the Skokomish River drainage dropped from an estimated 250 elk in the 1940s to ~25 animals in 1995 (Schwartz and Mitchell 1945). State and tribal cow harvest since 1980 was sufficient to cause recent population declines, though the decline seen from 1940-1980 was likely related to changes in habitat, primarily timber harvest patterns and resultant forage availability, as well as elk harvest. The PNPTC tribes closed tribal elk hunting in the Skokomish drainage in 1995, and in 1996 both WDFW and the tribes closed the entire GMU to elk hunting. As with the Dosewallips, the Skokomish herd remained static despite the hunting ban.

Because elk harvest appeared to be the proximate factor in recent populations declines, and habitat in both drainages seemed sufficient to support higher elk populations, a management decision to augment the small herds with translocated elk was made. Our goal was to evaluate the success of single augmentations of 17 elk translocated into the Dosewallips in 1995, and 24 elk translocated into the Skokomish in 1997. State and tribal managers agreed that the criteria for success was to increase each herd to ≥50 animals during the spring count. Monitoring of radio-collared cow elk from six herds on the east side of the Olympic Peninsula (referred to in this paper as resident elk) began in 1993 and provided baseline survival data needed for comparison (Smith et al. 1994). Our specific objectives were to 1) compare annual survival rates of resident and translocated elk, 2) evaluate movements of translocated elk, and 3) document the population response of the small herds in the Dosewallips and Skokomish drainages to the translocation.

## Study Area

The study area was located on the eastern portion of the Olympic Peninsula in northwest Washington, and consisted of portions of the Olympic (168,976 ha) and Skokomish (97,073 ha) GMUs (Figure 1). The source herd for the Dosewallips translocation was the non-migratory Dungeness herd located near Sequim, 37 km north of the Dosewallips River. The source herd used in the Skokomish translocation was a migratory herd that wintered near the Chehalis River, 56 km south of the Skokomish River.

Climate on the Olympic Peninsula is maritime, with dry summers and mild, wet winters. Annual precipitation averages 128 cm in the east, 63 cm in the north and 250 cm in the south Olympics, with differences due to the rain shadow effect of the Olympic Mountains (Henderson et al. 1989). Below 600 m snows are intermittent and fleeting with most precipitation falling as rain. Above 600 m snow is more persistent, and as a result, east Olympic elk winter below 600 m.

The study area was within the Western Hemlock (*Tsuga heterophylla*) Zone and included the western hemlock/salal (*Gaultheria shallon*), western hemlock/salal/sword fern (*Polystichum munitum*), western hemlock/salal-Oregongrape (*Berberis nervosa*), and western hemlock/sword fern-oxalis (*Oxalis oregana*) associations (Henderson et al. 1989). Land ownership was mixed, with lower elevations primarily held by large industrial timber companies and small private landowners. Higher elevations were in U.S. Forest Service and National Park Service ownership. Valley floors were largely residential or agricultural, often with pastures seeded in grasses, and the foothills were generally forested. Much of the forest in the lower valleys was clearcut harvested from the 1960s through the 1990s, and in 1995 there was a patchwork of recent clearcuts and young even-aged regeneration stands aged 10-40 yr. A limited number of late-successional patches were in the Forest Service ownership, primarily located in the Skokomish drainage.

Topography of both the Dungeness and Chehalis Rivers drainages, where the source herds were located, included relatively flat valley bottoms and

gently rolling hills. Elevation ranged from 6-15 m for the wintering Chehalis herd and 24-640 m for the resident herd at Dungeness. Habitat was chiefly grassy fields, riparian areas, wetlands, and some coniferous and deciduous forestland in various stages from recent clearcut to mature forest. The elk herds spent much of the time in agricultural fields and damage complaints were high in both drainages. However, hunting access was limited due to the proximity of residential areas, which precluded the use of state and tribal harvest as an effective method to reduce the elk herds.

Topography at the release sites in the Dosewallips and Skokomish drainages was characterized by steep valley walls and narrow valley floors. Elevations used by the resident herds ranged from sea level to 533 m in the Dosewallips and from 209-274 m in the Skokomish. The Skokomish differed from the capture sites and the Dosewallips because the resident herd did not occupy any residential or agricultural land.

## Methods

### Capture and Processing

We immobilized resident cow elk from six herds throughout the eastern Olympics using a dart rifle fired either from the ground or a helicopter. We collected canine tooth samples for age estimation using the cementum annuli technique, and attached Advanced Telemetry Systems (ATS) radio collars to cow elk (Hamlin et al. 2000). Each collar was equipped with a motion-sensitive mortality sensor. We placed numbered colored ear tags in all translocated elk, while resident elk did not receive ear tags. We processed resident elk at the site of capture, while translocated elk were transported to a processing station via helicopter. We released resident elk on site, and drove translocated elk in darkened stock trailers to the release site, where they were released as a group as close as possible to either the Dosewallips or Skokomish herd.

### Monitoring

We monitored resident and translocated elk with a combination of aerial and ground telemetry. For the first 2 mo after translocation, ground locations were gathered by triangulation (without direct observation) to minimize disturbance to the translocated elk. Subsequent ground locations consisted of either triangulation or direct observation to record location, total number of elk, herd composition, and number of ear-tagged elk in the herd. All locations were plotted on U.S. Geographical Survey 1:24,000 scale topographical maps. We replaced collars in each of the six resident herds as needed to maintain a minimum of two per herd, but collars on translocated elk were not replaced. Once a mortality signal was detected, we determined cause of death.

We collared 43 resident cow elk from the east Olympics and monitored them for survival 1993-2000. We conducted biweekly flights of these radio-collared elk from 1993-1995. Resident elk were relocated monthly from 1995-2000, either from the ground or air. Overall, we averaged 108 relocations/herd. We relocated elk translocated to the Dosewallips approximately biweekly from date of translocation to date of mortality (an average of 10 relocations) or until they joined the resident herd. We relocated elk released in the Skokomish weekly from April through June 1997 using ground telemetry and approximately once per month from June 1997 through September 1999 with aerial telemetry, averaging 32 relocations/elk.

### Data Analysis

We calculated annual survival rates for both the resident and translocated elk using a staggered-entry Kaplan-Meier survival estimator (Pollock et al. 1989). We used a 1-tailed z-test to test whether the annual survival rate of translocated cow elk was less than that of residents, using a minimum sample of five (Pollock et al. 1989). We calculated annual survival based on a 1 April to 31 March time period. Cause of mortality was placed into 4 categories: 1) predation (clear evidence of predation present), 2) unknown natural (no evidence of either predation or human-caused mortality), 3) human caused (evidence of bullets or arrows present), and 4) unknown (the carcass was too decomposed to reveal evidence of cause of mortality) (Smith et al. 1994). Significance levels for all tests were set at $P$=0.05.

We used ARCVIEW 3.0a (Environmental Systems Research Institute, Redlands, California) to analyze movements of translocated elk, and determined direction and distance of travel from release site to end point (either the mortality location or arithmetic center of the new home range) (White and Garrott 1990, Ruth et al. 1998, Zar 1999). Home range was calculated using a fixed

kernal estimator, using the least square cross validation method for the smoothing parameter (Worton 1989, Seaman et al. 1999). To test for possible homing behavior, we placed the end points of the translocated elk within one of four 90° quadrants centered on due north, south, east, and west from the release point. We then used chi-square to compare actual endpoints with expected non-directional dispersal from the release site.

We used the composition counts of the Dosewallips and Skokomish herds, obtained from ground surveys when herds were sighted in open habitat in February through April of each year, to document the minimum number in the herd. Because multiple counts from each herd were within 0-3 animals, we used the highest count as the minimum number present for each herd. Total population was not estimated because we had no reliable sightability factor. We also documented minimum spring numbers for the Dungeness herd (source population for the Dosewallips translocation), and as a comparison, the Duckabush herd, in the adjacent drainage located 2 km south of the Dosewallips. Both of these herds were also sighted in open fields, and had consistent multiple counts within 0-3 animals. We used a 1-tailed Mann Whitney U test to compare the minimum spring counts in the Dosewallips and Duckabush herds for 4 yr before and 5 yr after the translocation. We also compared spring counts from 3 yr prior and 5 yr post-translocation in the Dungeness herd and 4 yr prior and 2 yr post-translocation in the Skokomish herd.

## Results

### Survival

Seventeen elk (12 cows and 5 bulls) were translocated into the Dosewallips in April 1995, with no mortalities associated with the translocation procedure itself. Of the 17 translocated elk, three cows had a radio-collar attached. Two of the three radio-collared cows translocated to the Dosewallips died within the first 7 mo post-translocation. The small sample size precluded calculation of survival rates.

Twelve cows of 24 elk translocated into the Skokomish (20 cows and 4 bulls) in March 1997 were fitted with radio-collars. The collared cows had an average age of 5.4 yr (SE = 1.0), with a range from 2-14. Four mortalities occurred during the capture, which we did not include in the survival estimations because we were interested solely in survival post-translocation. No capture myopathy mortality was documented within the first month after the translocation. Annual survival rates for the 12 radioed cows translocated to the Skokomish averaged 0.65 (SE = 0.04) for the first 2 yr post-translocation (Table 1), and were significantly lower than resident elk in both years (1997-98: $P = 0.015$; 1998-99: $P = 0.003$). Survival in the third year did not differ significantly from that of residents.

Eleven of 15 (73%) translocated radio-collared elk (data combined from both the Dosewallips and Skokomish translocations) died from 1995-2000. Proximate causes of mortality for translocated elk included predation (30%), unknown natural mortality (30%), human caused (20%), and unknown (20%). Fourteen of the 43 (33%) radio-collared resident elk died from 1993-2000. Proximate causes of resident elk mortality included predation (25%), unknown natural mortality (31%), human caused (13%), and unknown (31%).

TABLE 1. Annual survival (April-March) for adult Roosevelt cow elk, from six resident herds in the east Olympics, 1993–2000, and 12 collared elk translocated into the Skokomish drainage, eastern Olympic Peninsula, Washington, 1997–2000. Non-significant differences in survival between resident and translocated elk during the same year are denoted by the same superscript letter.

| | Resident | | | Translocated | | |
|---|---|---|---|---|---|---|
| Year | n | Survival | SE | n | Survival | SE |
| 1993-94 | 15 | 1.0 | 0 | | | |
| 1994-95 | 22 | 0.82 | 0.02 | | | |
| 1995-96 | 23 | 0.78 | 0.02 | | | |
| 1996-97 | 22 | 0.86 | 0.01 | | | |
| 1997-98 | 16 | 0.94 | 0.01 | 12 | 0.67 | 0.03 |
| 1998-99 | 14 | 1.0 | 0 | 8 | 0.63 | 0.05 |
| 1999-00 | 19 | 0.95[a] | 0.01 | 5 | 0.80[a] | 0.07 |
| Mean 1993-00 | | 0.91 | 0.02 | | | |

### Movement

Of the 17 elk translocated to the Dosewallips, 7 (41%) remained with the target herd for ≥ 1 yr, 5 for ≥ 2 yr and 3 for ≥ 4 yr, as confirmed by multiple sightings of ear-tagged animals. One of the three radio-collared elk joined the Dosewallips herd immediately after the translocation and remained with the herd throughout the study period.

The early deaths of the other two precluded movement analysis.

None of the 12 radio-collared translocated elk joined the Skokomish herd, and only one ear-tagged bull of the 24 translocated into the drainage remained with that herd for 1 yr. Most moved out of the Skokomish drainage in the general direction of the capture site (Figure 2). These movements out of the drainage primarily occurred during the first 3 mo after translocation. Significantly more elk moved south, with 9 of the 12 elk movement endpoints located in the quadrant centered on due south ($P < 0.001$).

Elk translocated to Skokomish moved a mean distance of 20 km (range 1-42) from release site to end point. The two oldest collared elk (ages 14 and 8) died within 2 mo of the release date, and they had moved the shortest distance, remaining within the Skokomish drainage. With these elk omitted from the analysis, mean distance moved was 24 km (range 12-42 km). There was no correlation between the ages of the remaining collared elk and distance moved. By January 2000, only four of the 12 collared translocated elk survived, and each had joined a separate herd outside the Skokomish GMU. These four elk had moved the farthest, averaging 32 km to the center of their new home ranges.

### Population Response

The Dosewallips herd increased ($P = 0.01$) after the translocation, from a stable spring count of 23 from 1992-1995 to a mean of 51 (range 46-56) from 1996-2000 (Figure 3). The Dungeness source herd population did not differ significantly pre and post-translocation. The herd was estimated at 60 animals pre-translocation, recovered to 53 by 1997, and had a spring count of 68 in 1999.

Spring counts in the neighboring Duckabush resident herd had been slowly increasing from 1993-1995. Similar to the Dosewallips, the Duckabush population increased after the translocation date ($P = 0.01$), from 49 in 1995 to 73 in 1996, after which the numbers stabilized (Figure 3). None of the translocated elk joined this herd.

The Skokomish herd declined from 28 elk in 1992 to 17 in spring 1997. By spring 1998, 1 yr after the translocation, 25 animals were present. Both collars in the Skokomish herd were lost within 2 wk of each other in spring 1999 before a count could be obtained, and we were unable to get another count until fall 2000, when the herd was down to 15 animals (Figure 3). The Skokomish herd did not differ significantly before and after the translocation.

## Discussion

Augmenting a small elk herd in a single drainage depends on several factors, including adequate survival, fidelity of the translocated elk to the new area, and reproduction and growth rate of the resident herd. The survival of elk translocated into the Skokomish was significantly lower than resident herds in the east Olympics for the first 2 yr after the translocation, averaging 0.65 compared with the average 0.91 survival for resident elk from 1993-2000 (Table 1). The 0.65 survival of translocated elk was lower than the 0.77 reported for translocated elk in Oregon (Stussy et al. 1994). Several studies reviewed in Jones and Witham (1990) found that translocated white-tailed deer (*Odocoileus virginianus*) had lower survival than residents. Numerous other species also had poor survival after translocation (Erickson and McCullough 1981, Griffith et al. 1989). The translocation into the Skokomish likely disrupted normal elk herd behavior and social cohesiveness of the translocated elk, which may have contributed to lower survival. The elk moved long distances through unfamiliar territory, either singly or in small groups, which may have increased their vulnerability (Figure 2).

Movements of collared elk $\leq$3 mo after the translocation were representative of the other translocated elk, as ear-tagged elk were observed in similar locations to the radio-collared elk. The movement appeared to be homing behavior, because the endpoint of 9 out of 12 radio-collared elk was in the quadrant centered on due south (Figure 2). The Skokomish drainage runs east-west, and the topography to the north and south of the drainage is equally steep. The topography to the south does not become gentler until 14.5 km south of the river.

Possible explanations for the translocated elk not remaining within the Skokomish drainage include the predisposition of the source herd to migrate, disturbance from predators or people, and difference in habitat. Agricultural fields supplied a significant amount of nutrition to the highly productive Chehalis source herd, and were lacking in the Skokomish drainage. Of the four

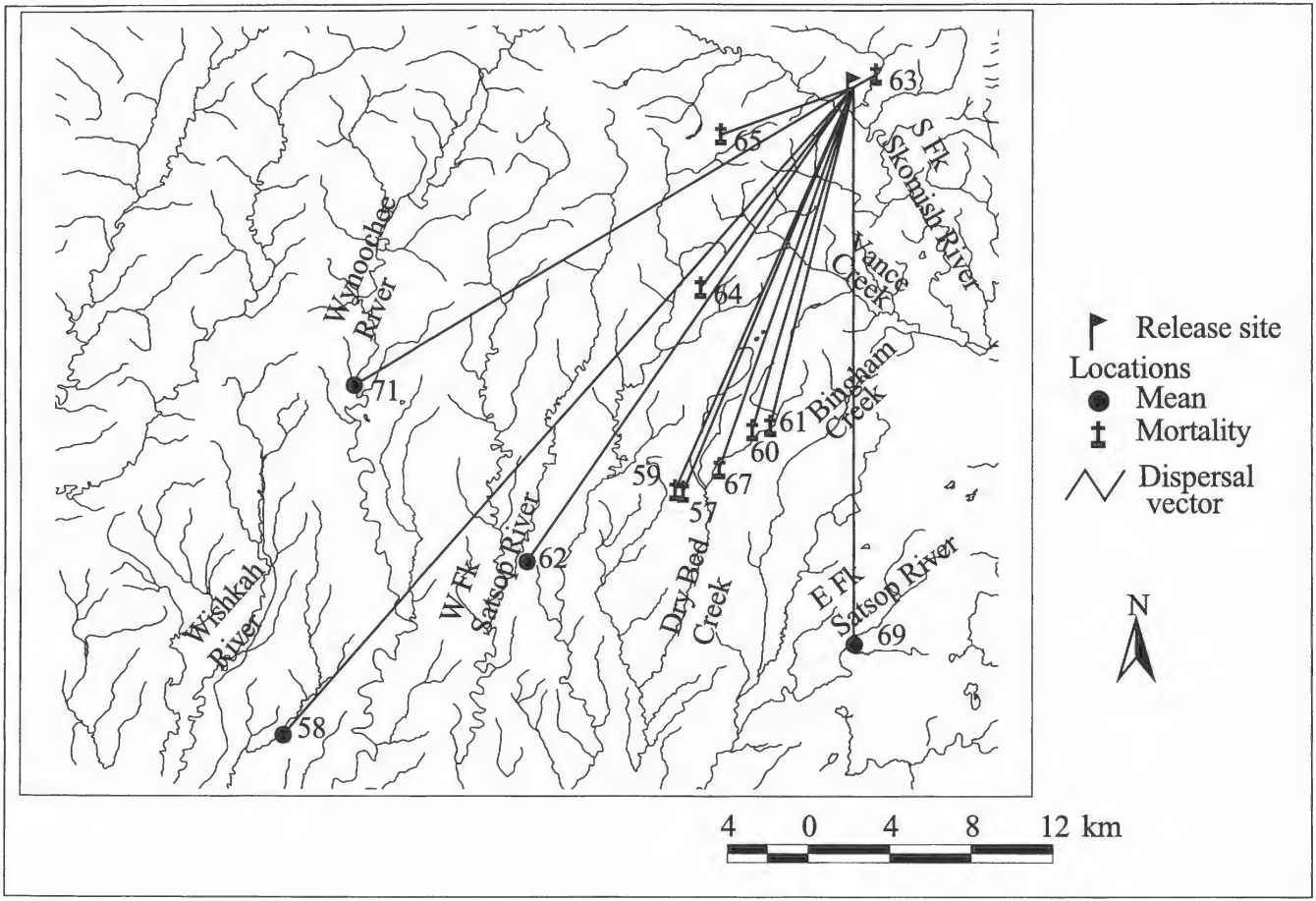


Figure 2. Direction of movement and distance traveled by translocated Roosevelt elk released in the Skokomish drainage, Olympic Peninsula, Washington, 1997.

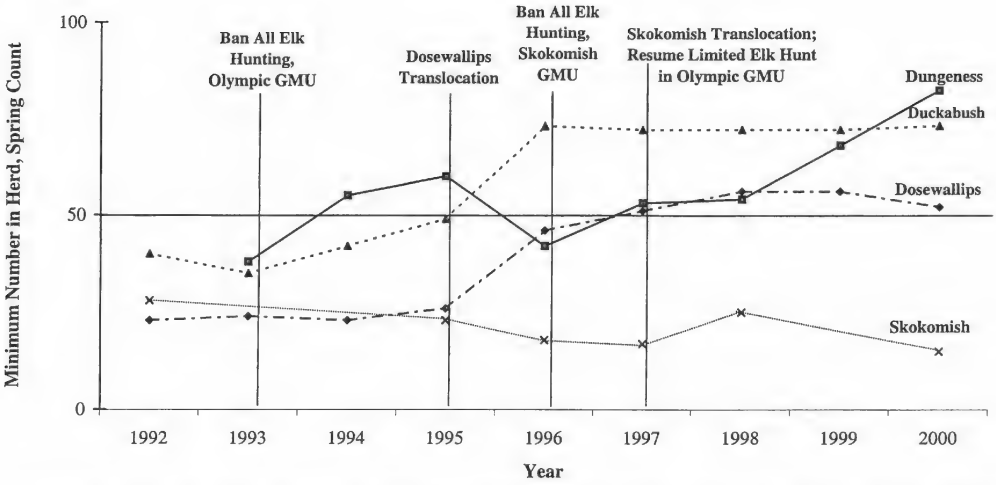


Figure 3. Minimum spring herd counts for the Dosewallips, Skokomish, Duckabush and Dungeness Roosevelt elk herds, before and after translocation, Olympic Peninsula, Washington.

surviving translocated collared elk, three remained in new home ranges that contained large fields. It is also possible that the amount of forage present in the Skokomish drainage was insufficient to support higher numbers of elk.

The Skokomish herd had a moderate increase from 17 to 25 animals 1 yr after the translocation, though only one translocated bull joined the resident herd (Figure 3). However, the count of 15 animals in 2000 is the lowest since it has been monitored, so that the single translocation was not effective in augmenting this herd and did not meet the criteria for success. The assumption that the habitat was sufficient to support higher numbers of elk may have been incorrect.

Site fidelity of the translocated Dosewallips group was greater than the Skokomish group. A possible reason may be that the habitat in the Dosewallips was not substantially different from that of the source Dungeness herd. Agricultural fields were used extensively in both drainages, and predator populations in the immediate area were likely low due to the proximity of human residences. Both of these factors probably contributed to the greater site fidelity seen in the Dosewallips group. In addition, the source herd was not migratory, so the translocated elk were not predisposed to large movements.

One year after the translocation, the Dosewallips herd, which had been stable at ≤25 animals prior to the translocation, almost doubled in size. However, other factors such as a high recruitment rate during the 1995-1996 season may have also played a role in the population increase. The closest neighboring herd to the Dosewallips, located in the Duckabush Valley, also had a dramatic population increase in 1995-1996 (Figure 3), indicating high recruitment in the east Olympics during that year. The increase to >50 animals in the Dosewallips herd met the criterion for success for the project developed prior to the translocation. Because both the Dosewallips and Duckabush herds have stabilized at higher numbers, the assumption that habitat could support higher numbers was supported.

## Management Implications and Recommendations

There were several disadvantages to translocating elk to supplement small local herds. It was expensive, with the cost estimated at about $450/animal moved, excluding staff time. It can cause elk mortality during the procedure and can result in lower survival after the translocation (Table 1). More importantly, the single translocation did not achieve the goal of supplementing the Skokomish herd, and other factors may have been important in the apparent success of the Dosewallips translocation.

Based on this study, we recommend: 1) complete a habitat analysis prior to a translocation effort, to ensure that sufficient habitat is available

to support additional animals, 2) habitat in the source and translocation areas must be similar, 3) the source herd should not be migratory, and 4) a large portion of the source herd should be moved, to retain herd dynamics and social cohesiveness. We also recommend that a soft release technique be considered, to increase site fidelity (Gogan and Barrett 1988, Phillips 1985). Supplemental feeding after the release may also help keep elk in the release area and reduce early dispersal (Witmer 1990). Multiple translocations may be required to supplement specific small herds that are not limited by habitat availability.

## Literature Cited


Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin 24:402-413.

Erickson, D. W., and C. R. McCullough. 1981. Fates of translocated river otters in Missouri. Wildlife Society Bulletin 15:511-517.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219-277 *In* J. W. Thomas and D. E. Toweill (editors), Elk of North America. Stackpole Books, Harrisburg, Pennsylvania.

Gogan, P. J. P., and R. H. Barrett. 1988. Lessons in management from translocations of Tule elk. Pages 275-287 *In* L. Nielsen and R. D. Brown (editors), Translocation of Wild Animals. Wisconsin Humane Society, Inc. and Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.

Griffith, B. J., M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477-480.

Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by 2 methods for Montana ungulates. Journal of Wildlife Management 64: 441-449.

Harper, J. A. 1987. Ecology and management of Roosevelt elk in Oregon. Unpublished report on file at Oregon Department of Fish and Wildlife, Portland, Oregon.

Henderson, J. A., D. H. Peter, R. D. Lesher, and D. C. Shaw. 1989. Forested Plant Associations of the Olympic National Forest. USDA Forest Service R6 Ecological Technical Paper 001-88. Pacific Northwest Region, Portland, Oregon.

Jones, J. M., and J. H. Witham. 1990. Post-translocation survival and movements of metropolitan white-tailed deer. Wildlife Society Bulletin 18:434-441.

Phillips, J. A. 1985. Acclimation of reintroduced Tule elk in the Diablo Range, California. M.S. Thesis, San Jose State University, San Jose, California.



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Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

Ruth, T. K., K. A. Logan, L. L. Sweanor, M. G. Hornocker, and L. J. Temple. 1998. Evaluating cougar translocation in New Mexico. Journal of Wildlife Management 62:1264-1275.

Schroer, G. L. 1986. Seasonal movements and distribution of migratory Roosevelt elk in the Olympic Mountains, Washington. M.S. Thesis, University of Washington, Seattle, Washington.

Schwartz, J. E., II, and G. E. Mitchell. 1945. The Roosevelt elk on the Olympic Peninsula, Washington. Journal of Wildlife Management 9:295-319.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Smith, J. L., W. A. Michaelis, K. Sloan, J. L. Musser, and D. J. Pierce. 1994. An analysis of elk poaching losses and other mortality sources in Washington using biotelemetry. Unpublished report on file at Washington Department of Fish and Wildlife. Olympia, Washington.

Stussy, R. J., W. D. Edge, and T. A. O'Neil. 1994. Survival of resident and translocated female elk in the Cascade Mountains or Oregon. Wildlife Society Bulletin 22:242-247.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. Journal of Wildlife Management 57:495-502.

White, G. C., and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego, California.

Witmer, G. 1990. Re-introduction of elk in the United States. Journal of the Pennsylvania Academy of Science 64:131-135.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall. Englewood Cliffs, New Jersey.

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# Crepuscular and Nocturnal Activity Patterns of Black Bears in the North Cascades of Washington

## Abstract

The activity patterns of radio-collared black bears were monitored during 1996-1998 at two study areas in the North Cascades of Washington. Compositional analysis of activity patterns showed that black bears were not equally active across time periods and that they exhibited crepuscular activity patterns regardless of sex, season, or study area. The lowest level of activity consistently occurred during the 0201-0400 PST time period. In general, females were most active during the morning and males during the evening. The results of this study suggest that diurnal telemetry data would adequately describe black bear resource use.

## Introduction

The activity patterns of animals are a result of the complex interactions between foraging efficiency, social activities, and environment (Aschoff 1964). An animal's pattern of activity and habitat use are adaptations to spatial and temporal variation in numerous environmental variables. The significance of these adaptations (Aschoff 1964, Neilsen 1983) makes it important to understand how diurnal, crepuscular, and nocturnal activities of animals influence habitat relationships. Most studies of space use by large carnivores use aerial telemetry because these species are wide ranging and often occupy rugged and remote areas. Habitat use estimates may be biased if sampling does not consider differences in a space use and activity patterns throughout a 24-hr period (Beyer and Haufler 1994).

Bear activity patterns have been determined by monitoring the integrity of radio-telemetry signals (Poekler and Hartwell 1973, Amstrup and Beecham 1976, Lindzey and Meslow 1977). Such determinations can be inhibited by radio interference, temperature fluctuations, and slight movements of bears (Garshelis and Pelton 1980, Garshelis et al. 1982). Theuerkauf and Jedrzejewski (2002) found that monitoring signal integrity alone overestimated the time wolves were active. However, using signal integrity, in combination with data on location changes obtained from triangulation, produced an accurate estimate of the activity patterns of wolves (Theuerkauf and Jedrzejewski 2002). This estimate was more accurate then activity sensors, which underestimated wolf activity (Theuerkauf and Jedrzejewski 2002).

Activity patterns have been reported for black bears on Long Island in southwestern Washington (Lindzey and Meslow 1977), on the Olympic Penninsula (Poekler and Hartwell 1973), and in west-central Idaho (Amstrup and Beecham 1976). In all of these areas bears have been reported as being the least active during the night. Laviviere et al. (1994) offered a possible explanation of the diurnal activity patterns of black bears in areas with low levels of human activity. They suggested that their excellent vision for details at close range and discrimination of colors (Bacon and Burghardt 1976a) results in more efficient foraging during daylight hours. Visual cues represent the primary mechanism in searching for food (Bacon and Burghardt 1976b).

We monitored the crepuscular and nocturnal activity patterns of black bears to evaluate how well diurnal telemetry data would describe habitat use. The crepuscular and nocturnal activity patterns of black bears have not been described in the North Cascades of Washington, and may have important implications relative to their management. Our research questions included: (1) Are black bears equally active across all crepuscular and nocturnal time periods? (2) Do black bear activity patterns vary between study areas and seasons? (3) Are male and female black bear activity patterns similar?

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## Study Areas

This study was conducted in the Okanogan Study Area (OSA) on the eastern side of the Cascade mountain crest and the Snoqualmie Study Area (SSA) on the western side (Figure 1). Elevations within the study areas ranged from 100 m in the valley bottoms to 2500 m at the ridge crests.

Precipitation on the OSA, falling mostly as snow, ranged from an average of 150-200 cm/yr on the ridge crests to 25-50 cm/yr in the lower elevations. Precipitation on the SSA, falling mostly as rain, ranged from 170-300 cm/yr. Vegetation conditions on the OSA varied from open bitterbrush *(Purshia tridentata)* slopes on the low elevation eastern portion of the study area, to Douglas-fir *(Pseudotsuga menziesii)* and ponderosa pine *(Pinus ponderosa)* forests at the lower and mid elevations, to montane and alpine vegetation beginning at about 1500 m. The SSA was composed of a mosaic of clearcuts and second growth western hemlock *(Tsuga heterophylla)* forests on the lower elevations, extending to montane and alpine vegetation above about 1200 m.

## Methods

Black bears were captured and fitted with radio transmittters during April-July 1994-1997 (details described in Koehler et al. 2001). Each captured bear was ear-tagged and the upper lip was tatooed with an unique identifying number. Total body length, chest girth, and weight were measured. A premolar was extracted to determine age, and blood

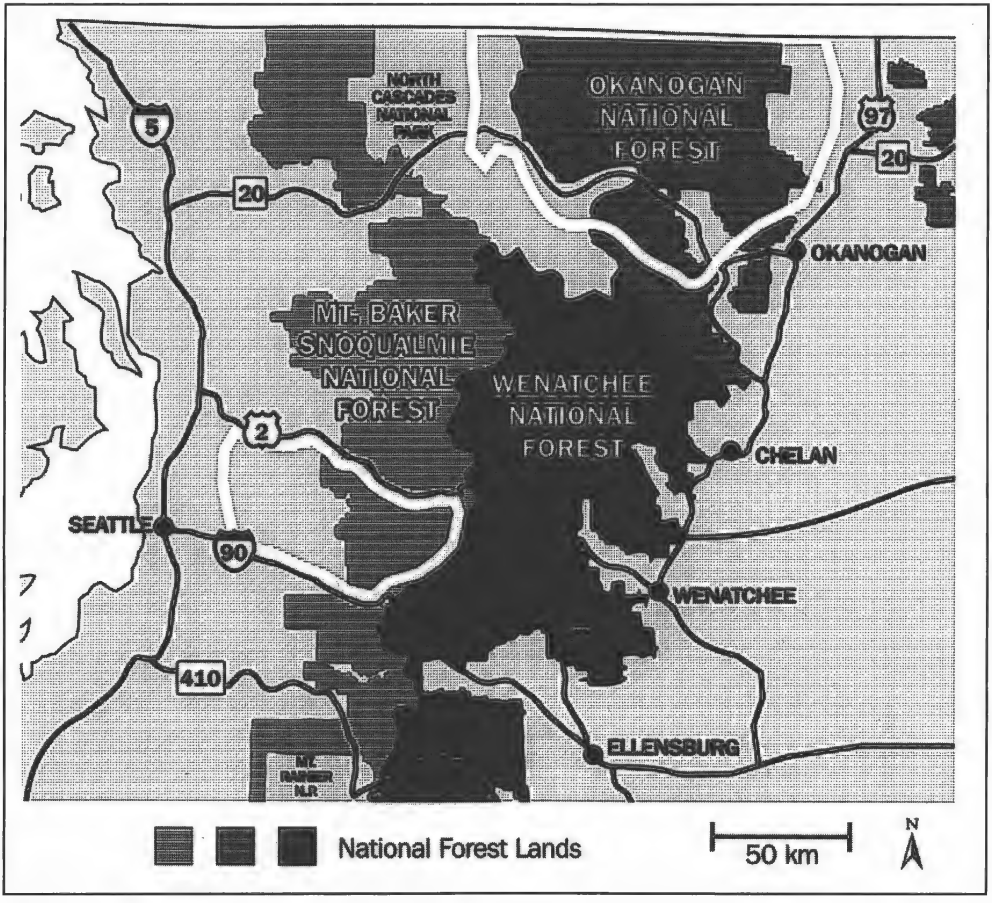


Figure 1. The Okanogan and Snoqualmie study areas are outlined in white.

was collected to assess disease and develop DNA profiles.

The crepuscular and nocturnal activities of radio-collared black bears were monitored using signal integrity and triangulation approximately one night per week, from den emergence to den entrance. On the OSA, bears were monitored during 1996 and 1997, and on the SSA during 1998. Bears were generally monitored from roads due to safety considerations. Each night from 1-4 bears were monitored at 2 hr intervals from 2000 PST to 0800 PST. Telemetry signals were monitored for 2-3 min from two locations for a total of 5-6 min/2 hr time period (Altmann 1974, Lariviere et al. 1994). Bearings to each bear were taken from 2-3 known locations along roads or trails within 10 min of each other to minimize bear movements. If there was any chance of disturbing the bear, only the signal integrity was monitored. Consecutive bearings between time periods were compared to determine if the bear had moved. A bear was considered active for a time period if the intensity of the signal was uneven or the bear had changed its location since the last radio location (Theuerkauf and Jedrzejewski 2002).

Data were analyzed by compositional analysis (Aebischer et al. 1993) using the computer program RESELECT. Compositional analysis uses multiple analysis of variance (MANOVA) to test the hypotheses, and paired t-tests to rank the relative levels of activities within each time period (Aebischer et al. 1993). Multiple pairwise comparisons were made to determine if any time periods were used significantly more than others. The significance level for all tests was set at $P = 0.05$. Seasons were determined by observed changes in bear diets and plant phenology. Seasons were divided into early-season (den emergence to 31 July), and late-season (1 August to den entrance).

We described activity patterns for 21 black bears (11 females and 10 males). Bears were monitored over 76 12-hr monitoring sessions, for a total of 912 hr between 1996 and 1998 (Table 1). Five tests using humans with radio collars were initially used to validate the results of the activity monitoring and none of these tests resulted in erroneous activity classifications.

## Results

### Annual Activity Patterns

Data from 21 black bears (11 females and 10 males) showed that their activities were not equally distributed across the time periods (Wilks lambda=0.11, $P<0.0001$) (Figure 2). Bears were the least active during the 0201-0400 time period and the most active during the crepuscular time periods (Table 2). Female black bears (6 from the OSA, 5 from the SSA) were least active during 0201-0400 and were most active during 0601-0800 (Wilks lambda=0.06, P<.0001, Table 2). Likewise, male black bears (8 from the OSA, 2 from the SSA) were least active during the same time period as the females (Wilks lambda=0.07, P<0.0001, Table 2). However, the highest level of activity for males occurred in the 2000-2200 time period. This information suggests that males were more active during the evening hours and females in the morning hours.

### Okanogan vs Snoqualmie Study Areas

Black bears on the OSA (6 females and 7 males, Wilks lambda=0.09, $P<0.0001$) and SSA (5 females and 2 males, Wilks lambda=0.01, $P<0.0001$) exhibited crepscular activity patterns (Table 2). Black bears on the OSA were more active during 0601-0800 and 2000-2200 than during the other time periods, exhibiting a stronger crepuscular pattern than on the SSA. On the SSA, fewer sta-

TABLE 1. Summary information for crepuscular and nocturnal black bear activity pattern monitoring on the Okanogan and Snoqualmie study areas in the North Cascades, Washington.

| Year | Study area | Total | No. Female | No. Male | Hours Monitored | Nights Monitored |
|---|---|---|---|---|---|---|
| 1996 | Okanogan | 8 | 3 | 5 | 348 | 29 |
| 1997 | Okanogan | 14 | 7 | 7 | 360 | 30 |
| 1998 | Snoqualmie | 7 | 5 | 2 | 204 | 17 |
| Totals | | 21 | 11 | 10 | 912 | 76 |

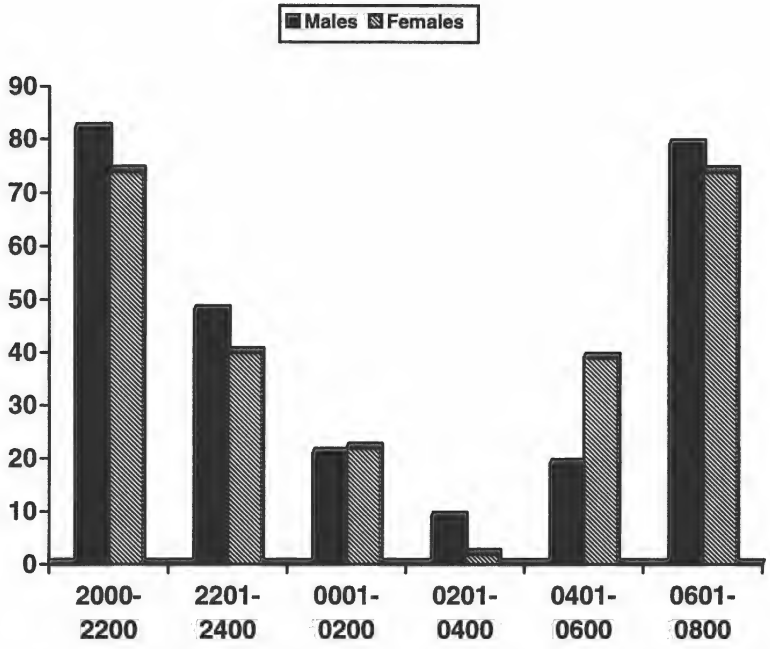


Figure 2. The proportion of radio-collared black bears active during the crepuscular and nocturnal time periods, North Cascades, Washington, 1996-1998.

tistically significant differences occurred between activity levels among time periods.

### Seasonal Activity Patterns

Data from 19 black bears (9 females and 10 males) were used to investigate their activity patterns during the early-season. The activity patterns of black bears during the early-season indicated that bears were crepuscular (Wilks lambda=0.05, $P<0.0001$). During 0201-0400 black bear activity levels were lower than during any other time period (Table 3). The highest levels of activity occurred during 2000-2200 and 0601-0800.

The activity patterns of 14 black bears (10 females and 4 males) during the late-season showed that black bear activity was highest during crepuscular time periods (Wilks lambda=0.10, $P<0.0001$). However, during the late-season black bears were most active during the morning hours (Table 4), a shift from the early-season.

### Male vs Female

Female activity levels (n=9, Wilks lambda=0.06, $P=0.0001$) were lower during 0001-0200 and 0201-0400 than other time periods. The highest levels of activity occurred during 0601-0800. Males were the least active during the nocturnal time periods and most active during the evening in the early-season (Wilks lambda=0.02, $P<0.0001$). While not a statistical relationship, this information suggests that black bears were segregated by gender at some level during the early-season.

Female black bears were most active in the late-season during 0401-0600 and 0601-0800 (n=10, Wilks lambda=0.01, $P<0.0001$). During both seasons, females were most active during the morning hours. Samples sizes for males during the late-season were too small for analysis.

## Discussion

The annual and seasonal activity patterns of black bears in this study were similiar to those reported for black bears in other studies in the northwestern USA where bears have been reported as being generally diurnal, and most active during the morning and evening. (Amstrup and Beecham 1976, Lindzey and Meslow 1977, Poekler and Hartwell 1973). However, black bears may become

TABLE 2. Results of the multiple comparisons of annual black bear activity patterns among the six time periods, 1996-1998. + and – indicate that the time period on the left hand column had significantly higher or lower activity than the time period on the top row, $P = 0.05$. Rankings: 0 = least used time period, 5 = most used time period.

| | | Time Periods | | | | | |
|---|---|---|---|---|---|---|---|
| Rankings | Time Periods | 2000-2200 | 2201-2400 | 0001-0200 | 0201-0400 | 0401-0600 | 0601-0800 |
| **Females (n = 11)** | | | | | | | |
| 4 | 2000-2200 | | | + | + | | |
| 2 | 2201-2400 | | | | + | | |
| 1 | 0001-0200 | – | | | | – | – |
| 0 | 0201-0400 | – | – | | | – | – |
| 3 | 0401-0600 | | | + | + | | – |
| 5 | 0601-0800 | | + | + | + | | |
| **Males (n = 10)** | | | | | | | |
| 5 | 2000-2200 | | | + | + | + | |
| 4 | 2201-2400 | | | + | + | + | |
| 1 | 0001-0200 | – | – | | | | |
| 0 | 0201-0400 | – | – | | | – | – |
| 2 | 0401-0600 | – | – | | + | | |
| 3 | 0601-0800 | | | | + | | |
| **Okanogan (7 females and 7 males)** | | | | | | | |
| 4 | 2000-2200 | | + | + | + | | |
| 3 | 2201-2400 | – | | + | + | | – |
| 1 | 0001-0200 | – | – | | | | – |
| 0 | 0201-0400 | – | – | | | – | – |
| 2 | 0401-0600 | | | | + | | – |
| 5 | 0601-0800 | | + | + | + | + | |
| **Snoqualmie (5 females and 2 males)** | | | | | | | |
| 4 | 2000-2200 | | | | + | | |
| 3 | 2201-2400 | | | | + | | |
| 1 | 0001-0200 | | | | | | |
| 0 | 0201-0400 | – | – | | | | – |
| 2 | 0401-0600 | | | | | | |
| 5 | 0601-0800 | | | | + | | |

TABLE 3. Results of the multiple comparisons of early-season (den emergence to 31 July) black bear activity patterns among the six time periods, 1996-1998. + and – indicate that the time period on the left hand column had significantly higher or lower activity than the time period on the top row, $P = 0.05$. Rankings: 0 = least used time period, 5 = most used time period.

| | | Time Periods | | | | | |
|---|---|---|---|---|---|---|---|
| Rankings | Time Periods | 2000-2200 | 2201-2400 | 0001-0200 | 0201-0400 | 0401-0600 | 0601-0800 |
| **Both Study Areas (9 females and 10 males)** | | | | | | | |
| 5 | 2000-2200 | | + | + | + | | |
| 3 | 2201-2400 | – | | + | + | | |
| 1 | 0001-0200 | – | – | | + | | – |
| 0 | 0201-0400 | – | – | – | | – | – |
| 2 | 0401-0600 | – | | | + | | – |
| 4 | 0601-0800 | | | + | + | + | |

TABLE 4. Results of the multiple comparisons of late-season (1 August-den entrance) black bear activity patterns among the six time periods, 1996-1998. + and – indicate that the time period on the left hand column had significantly higher or lower activity than the time period on the top row, $P = 0.05$. Rankings: 0 = least used time period, 5 = most used time period.

| | | Time Periods | | | | | |
|---|---|---|---|---|---|---|---|
| Rankings | Time Periods | 2000-2200 | 2201-2400 | 0001-0200 | 0201-0400 | 0401-0600 | 0601-0800 |
| **Both Study Areas (10 females and 4 males)** | | | | | | | |
| 4 | 2000-2200 | | + | + | + | | |
| 2 | 2201-2400 | – | | | | | – |
| 1 | 0001-0200 | – | | | | – | – |
| 0 | 0201-0400 | – | | | | – | – |
| 3 | 0401-0600 | – | | + | + | | |
| 5 | 0601-0800 | | + | + | + | | |

nocturnal to reduce competition with grizzly bears (MacHutchon et al.1998) or when habituated to human activities (orchards, garbage dumps, campgrounds) (Ayres et al.1986). No evidence was available to suggest that black bears in this study were feeding on human foods, and grizzly bear numbers in the North Cascades are likely too low (Almack et al. 1993, Gaines et al. 2000) to influence black bear activity patterns.

The annual and seasonal activity patterns of black bears in this study suggested that males were more active during the evening and females during the morning. Garshelis and Pelton (1980) reported that adult males were overall more active than solitary adult females, but they did not describe any segregation of activity patterns by gender. Further research is needed to quantify this relationship.

Garshelis and Pelton (1980) reported nocturnal bear activity may increase during the fall. This was not the case in this study as black bears exhibited crepuscular activity patterns in both study areas, regardless of their sex or the season. Our research showed that black bears were relatively inactive during the night. Therefore, diurnal telemetry locations collected when bears are active should be used to evaluate their habitat use. Habitat managers should have confidence that habitat use analysis based on a diurnal telemetry dataset would identify all the important habitats for bears, thus addressing the issues raised by Beyer and Haufler (1994).

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## Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Almack, J. A., W. L. Gaines, R. H. Naney, P. H. Morrison, J. R. Eby, G. F. Wooten, M. C. Snyder, S. H. Fitkin, and E. R. Garcia. 1993. North Cascades Grizzly Bear Ecosystem Evaluation: unpublished final report. Interagency Grizzly Bear Committee, Denver, Colorado.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-267.

Amstrup, S. C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. Journal of Wildlife Management 40:340-348.

Aschoff, J. 1964. Survival value of diurnal rhythms. Symposium Zoological Society of London 13:59-98.

Ayres, L. A., L. S. Chow, and D. M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. International Conference on Bear Research and Management 6:151-154.

Bacon, E. S., and G. M. Burghardt. 1976a. Ingestive behaviors of the American black bear. International Conference on Bear Research and Management 3:13-25.

Bacon, E. S., and G. M. Burghardt. 1976b. Learning and color discrimination in the American black bear. International Conference on Bear Research and Management 3:27-36.

Beyer, D. E., and J. B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. Journal of Wildlife Management 58:178-180.

Gaines, W. L., P. Singleton, and A. L. Gold. 2000. Conservation of rare carnivores in the North Cascades Ecosystem, Western North America. Natural Areas Journal 20:366-375.

Garshelis, D. L., and M. R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. Journal of Mammalogy 61:8-19.

Garshelis, D. L., H. B. Quigley, C. R. Villarrubia, and M. R. Pelton. 1982. Assessment of telemetric motion sensors for studies of activity. Canadian Journal of Zoology 60:1800-1805.

Koehler, G. M., P. Briggs Hall, M. H. Norton, and D. J. Pierce. 2001. Implant- versus collar-transmitter use on black bears. Wildlife Society Bulletin 29:600-605.

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Lariviere, S., J. Huot, and C. Samson. 1994. Daily activity patterns of female black bears in a northern mixed-forest environment. Journal of Mammalogy 75:63-620.

Lindzey, F. G., and E .C. Meslow. 1977. Home range and habitat use by black bears in southwestern Washington. Journal of Wildlife Management 41:413-425.

MacHutchon, A. G., S. Himmer, H. Davis, and M. Gallagher. 1998. Temporal and spatial activity patterns among coastal bear populations. Ursus 10:539-546.

Nielsen, E .T. 1983. Relation of behavioral activity rhythms to the changes of day and night. A revision of views. Behaviour 89:147-173.

Poelker, R. J., and H .D. Hartwell. 1973. Black bear of Washington: its biology, natural history and relationship to forest regeneration. Washington Department of Game, Biological Bulletin No. 14. Olympia, Washington.

Theuerkauf, J., and W. Jedrzejewski. 2002. Accuracy of radiotelemetry to estimate wolf activity and locations. Journal of Wildlife Management 66:859-864.

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# Fire History in Coast Redwood Forests of the Mendocino Coast, California

## Abstract

We reconstructed fire history in old-growth coast redwood stands along an ocean-to-inland gradient in Jackson Demonstration State Forest on the Mendocino Coast in northern California. Fire history was reconstructed for the past two to four centuries using fire scars recorded in tree rings. Surface fires were frequent disturbances in all stands prior to the early twentieth century. Composite mean fire-free intervals aggregated within stands varied from 6 to 20 yr, and point mean fire-free intervals averaged within trees varied from 9 to 20 yr. Fires ceased in the early 20th century coincident with the advent of organized fire suppression efforts beginning in the 1930s. Fire frequency did not vary significantly along the ocean-inland gradient. Although several of the inland stands tended to record shorter intervals between fires, there was high variability among sites. These and analogous fire-scar data from other studies across the range of coast redwood forests suggest that fire frequencies have been underestimated in some past assessments. A principal reason is that fire-scar records on coast redwood trees are difficult to locate because of inadequate preservation compared to other species that experienced surface fires. Cessation of surface fires has resulted in shifts in fuel and forest structure over recent decades, and the fire history reconstructed by this study provides both guidelines and justification for ecological restoration efforts in coast redwood forests of this region.

## Introduction

Fire has long been recognized as an important disturbance in coast redwood (*Sequoia sempervirens*) forests (Fritz 1931), but the exact nature of historical fire regimes in many areas is uncertain. Coast redwood grows in relatively mesic, often fog-shrouded coastal locations not usually associated with widespread or frequent fires. Past studies and reviews of coast redwood fire ecology have concluded that, over much of its range, fires were typically infrequent and that effects on forest composition and structure varied depending primarily on fire severity (Veirs 1980, 1982, 1996; Wright and Bailey 1982; Agee 1993; Sawyer et al. 2000a). However, a growing body of evidence documents that frequent, episodic surface fires were the dominant fire regime in many coast redwood forests, and that loss of surface fires has occurred over the recent century in response to loss of Native American ignition sources, active fire suppression, and other changes in land use (Finney 1990; Finney and Martin 1989, 1992; Brown and Swetnam 1994; Brown et al. 1999).

Differences seen in fire regimes reconstructed by various studies are likely related both to site conditions that vary along ocean-to-inland gradients and with latitude (Veirs 1982, Stuart 1987, Agee 1993, Sawyer et al. 2000a) and to the differing methods used to reconstruct fire histories (Finney and Martin 1989, Brown and Swetnam 1994). Fire histories based mainly on aging of coast redwood or substory canopy trees have typically found that fires were infrequent and relatively severe, with recurrence intervals of ca. 20 to > 500 yr (Veirs 1980, 1982, 1996; Stuart 1987). Other studies examined fire scars to reconstruct relatively long intervals recorded on individual trees, with ranges from ca. 20 to > 50 yr between mixed-severity fires (Fritz 1931, Jacobs et al. 1985, Stuart 1987). Other fire-scar studies used data composited from several trees to reconstruct high surface fire frequencies in some areas, with mean recurrence intervals from 7 to 15 yr depending on site conditions and period analyzed (Finney 1990; Finney and Martin 1989, 1992; Brown and Swetnam 1994; Brown et al. 1999).

Defining the historical nature of fire has important implications for understanding ecological dynamics and guiding sustainable management in coast redwood forests (Jacobs et al. 1985,

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Thornburgh et al. 2000). Ecologists and managers increasingly rely on historical data to assess forest conditions over longer time scales than are available from direct observations (Morgan et al. 1994, Landres et al. 1999). Fire was an especially ubiquitous disturbance in many forests for many centuries to millennia, but historical patterns have been disrupted over the recent century by changes in land use and active fire suppression (Covington et al. 1994). Cessation of Native American burning in coastal California forests (Lewis 1973) also contributed to a general loss of historical fire regimes from this area. Changes in fire regimes in coastal forests have resulted in associated changes in vegetation patterns, such as increases in tree density and invasion of woodlands and forests into areas that were historically grass or shrub ecosystems (Brown et al. 1999). Some ecologists have suggested that coast redwood should be considered a climax species and fire-independent (Fritz 1931, Roy 1966, Wright and Bailey 1982) whereas others contend that fire is a necessary component in coast redwood ecology (Cooper 1965, Stone et al. 1972) and should be reintroduced in parks and other natural areas (Jacobs et al. 1985).

In this study, we report on an ocean-to-inland gradient of fire-scar collections from coast redwood forests in Jackson Demonstration State Forest on the Mendocino Coast in northern California. We reconstructed fire history for the past two to four centuries in seven stands to test a hypothesis that fire frequency varied from mesic coastal forests to drier inland stands (Veirs 1980, 1982). Veirs (see also Sawyer et al. 2000a) proposed that fire varied from greater than 250-yr recurrence intervals at often fog-shrouded coastal sites to ca. 50-yr intervals in inland mixed coast redwood - Douglas-fir (*Pseudotsuga menziesii*) forests. Our objectives for this study are to provide detailed fire histories from this area of the California coast and to help further define the historical role of fire in coast redwood forests throughout its range.

## Methods

### Study Area

Jackson Demonstration State Forest was established in 1947 to demonstrate and research timber harvest methods and impacts in coast redwood-Douglas-fir forests of the northern California coast (Figure 1). The area that includes the 20,316 ha state forest has had a history of continuous timber production since the 1860s (Wurm 1986), and only a few areas of residual old-growth forest exist (Henry 1998). Clear-cut logging was exclusively used as a harvest method until the mid-twentieth century. Current forests typically consist of dense stands of second-growth coast redwood, Douglas-fir, western hemlock (*Tsuga heterophylla*), and grand fir (*Abies grandis*) (Henry 1998). Substory hardwood tree species include tanoak (*Lithocarpus densiflora*) and red alder (*Alnus rubra*), and

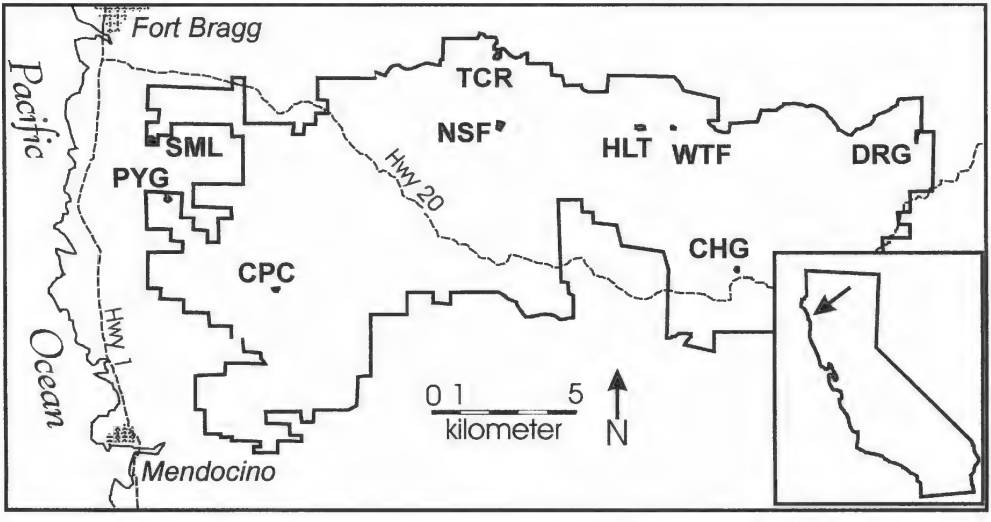


Figure 1. Locations of fire-scar collections at Jackson Demonstration State Forest. Refer to Table 1 for key to abbreviations.

understory shrub species include huckleberry (*Vaccinum* spp.), Pacific rhododendron (*Rhododendron macrophyllum*), and sword fern (*Polystichum munitim*). Overstory dominance by coast redwood generally decreases from west to east, and forests are fringed on the west by a band of coastal shrub and grasslands. Soil nutrient-poor terraces along the coast also support unique pygmy forests of stunted pines and cypress (Westman and Whittaker 1975). Coast redwood often forms pure stands in drainage bottoms or in more moist areas, but is intermixed with other species on slopes and dryer locations.

Coast redwood occurs along a relatively narrow coastal band from central California south of Monterey Bay to the extreme southwestern coast of Oregon (Roy 1966). Coast redwood forests experience a Mediterranean climate with mild, wet winters and cool, dry summers. The distribution of coast redwood in coastal mountain ranges and valleys corresponds closely to the presence of oceanic fogs that reduce evapotranspirative stress during otherwise dry summer months (Dawson 1998). Annual temperature fluctuations on the coast also are moderated by the oceanic influence relative to inland locations (Figure 2). In addition to moisture gradients that occur with distance from the ocean, three major subregions of coast redwood have been defined based on moisture regimes and forest structure (Sawyer et al. 2000b). The Mendocino Coast is in the central subregion, and coast redwood forests here are compositionally and ecologically more similar to inland Douglas-fir-tanoak forests than to coast redwood forests of the generally moister northern subregion that have affinities with northwestern coastal forests (Agee 1993, Sawyer et al. 2000b).

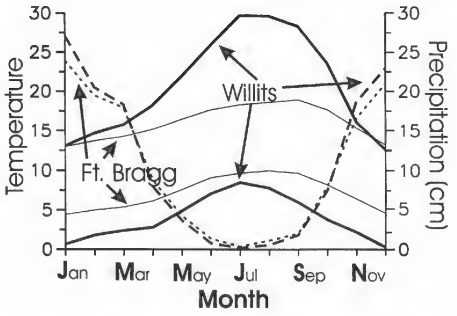


Figure 2. Climate summaries for Ft. Bragg on the coast (light lines), and Willits, 39 km inland (heavy lines). Mean monthly maximum and minimum temperatures (solid lines) and total precipitation (dashed lines) are from Western Regional Climate Center (2002).

Prior to Euro-American settlement that began in this area in the mid-nineteenth century, many (if not most) historical fires were likely set by humans. Lightning during the historic period has been rare on the California coast, especially compared to other regions in California (Program for Climate, Ecosystems, and Fire Applications 2002). References to Native American burning practices are extensive (Lewis 1973, Boyd 1999), and coastal tribes were known to have set fires for clearing brush, hunting, or accidentally.

## Selection of Sites and Trees for Reconstruction of Fire History

We selected stands for reconstruction of fire history based on the presence of living old-growth coast redwood trees (Figure 1, Table 1). All stands had predominantly or exclusively coast redwood overstory. We surveyed known patches of residual

TABLE 1. Fire history sites at Jackson Demonstration State Forest.

| Site | Site code | Elev. (m) | Dist. from ocean (km) | Slope (deg) | Aspect | Site area (ha) | No. of trees collected/aged |
|---|---|---|---|---|---|---|---|
| Simpson Lane | SML | 82 - 98 | 2.8 | <5 | W | 18.6 | 15/0 |
| Pygmy Forest | PYG | 94 - 110 | 3.2 | <5 | NW | 6.2 | 9/6 |
| Caspar Creek | CPC | 195 - 213 | 8.0 | 5-10 | W | 12.8 | 8/0 |
| N. Fork of the S. Fork | NSF | 350 - 398 | 14.7 | 20-25 | N | 10.0 | 8/4 |
| Three-Chop Ridge | TCR | 350 - 384 | 14.7 | 20-25 | S | 10.8 | 6/3 |
| High-Low Trestle | HLT | 366 - 421 | 19.3 | 35-45 | S | 22.0 | 32/14 |
| Waterfall Grove | WTF | 280 - 338 | 20.3 | 0-40 | S | 16.9 | 18/8 |
| Chamberlain Grove | CHG | 219 - 244 | 22.1 | 10-30 | SE | 5.6 | 15/8 |
| Dresser Grove | DRG | 314 - 366 | 27.8 | 10–15 | N | 14.5 | 15/5 |
| Total trees collected/aged | | | | | | | 126/48 |

old-growth forest at JDSF for either living trees or stumps with sequences of fire scars that resulted from repeated surface fires. We also surveyed several harvested areas but were not able to find suitable fire-scar records. Stumps were typically heavily decayed and charred from past broadcast burning that took place during logging operations (Wurm 1986). Random selection of sites was, therefore, not possible because of the extreme rarity of preservation of appropriate fire-scar data both across the JDSF landscape and on individual trees. As with other paleoecological data (e.g., pollen sequences, fossil assemblages), adequately preserved paleo-fire records are patchily distributed and directed sampling had to be employed to derive a useful data set. However, because of the arbitrary nature of preservation of the residual old-growth stands where we reconstructed fire histories, we consider the distribution of our sites to be randomly placed across the landscape and, thus, likely representative of landscape patterns of fire occurrence over the past few centuries.

Once trees with fire-scar records were found, we used a chainsaw to cut partial transverse cross sections from a location with the most visible fire scars. On several trees, more than one cross section was cut in an effort to obtain more complete sequences. Our goal during sampling was to compile inventories of fire events from fire scars recorded on 8 to 30+ trees in stands 4-20 ha in size for as far back in time as fire-scar records could be found (Swetnam and Baisan 1996, Brown et al. 2001). Our population of interest for fire frequency analysis consists of fire events that occurred prior to extensive logging that began in this area in the 1860s.

### Development of Fire Chronologies

All wood samples were prepared and surfaced such that cellular structure was visible in tree rings. We attempted to crossdate tree-ring series using skeleton plots (Stokes and Smiley 1968) and cross-correlations of measured ring widths (Brown and Swetnam 1994). Unusually narrow and wide rings and locations of fire scars were marked on skeleton plots made for each cross section (also see methods in Finney and Martin 1989 and Brown and Swetnam 1994). We also recorded positions of fire scars within ring series, which is an indication of seasonal timing of past fires. Ring widths on selected radii of some cross sections were measured using a moveable stage connected to a linear encoder. Cross correlations of measurements between radii were calculated using program COFECHA (Holmes 1983). Skeleton plots and measured ring widths were compared to each other, to those made from living unscarred Douglas-fir in the same stands, and to existing tree ring-width chronologies and reconstructions of Palmer drought severity indices (PDSI) for this area of northern California (National Geophysical Data Center 2002).

We compiled approximate fire dates for all fire-scarred trees in each stand into fire chronologies using program FHX2 (Grissino-Mayer 2001). FHX2 is an integrated package for graphing and statistical analyses of fire-scar data. Fire frequencies for different periods of the fire chronologies were estimated using mean fire intervals (MFI) and Weibull median probability intervals (WMPI) (Grissino-Mayer 1999). Variability in fire intervals is reported as the first standard deviation and range of intervals. We also calculated mean point fire intervals based on fire intervals recorded within individual trees. We used regression analysis to assess whether there were significant differences in composite and point MFIs along the ocean-inland gradient.

## Results

### Fire Chronologies

We determined approximate fire-scar dates on 48 trees from 7 stands out of a total of 126 trees sampled from 9 stands (Table 1, Figure 3). We were unable to determine fire-scar dates on many trees because of the often extreme tightness of ring series that made ring counts unreliable. On other trees, fire-scar sequences were too eroded by decay or past burning of the scarred surfaces (Figure 4), and fire dates were available back to only the late 19th century at the earliest. Two of the sites (SML and CPC) lacked fire dates to calculate pre-harvest fire frequency.

Certainty in crossdating was not possible in any coast redwood samples, generally because tree rings tended to be complacent with little variability in ring widths or other climatically-controlled morphological characteristics with which to cross-match with other trees in a stand or area (Fritz and Averill 1924, Fritz 1940, Schulman 1940, Brown and Swetnam 1994). Tree rings in coast redwood trees also often end abruptly for no

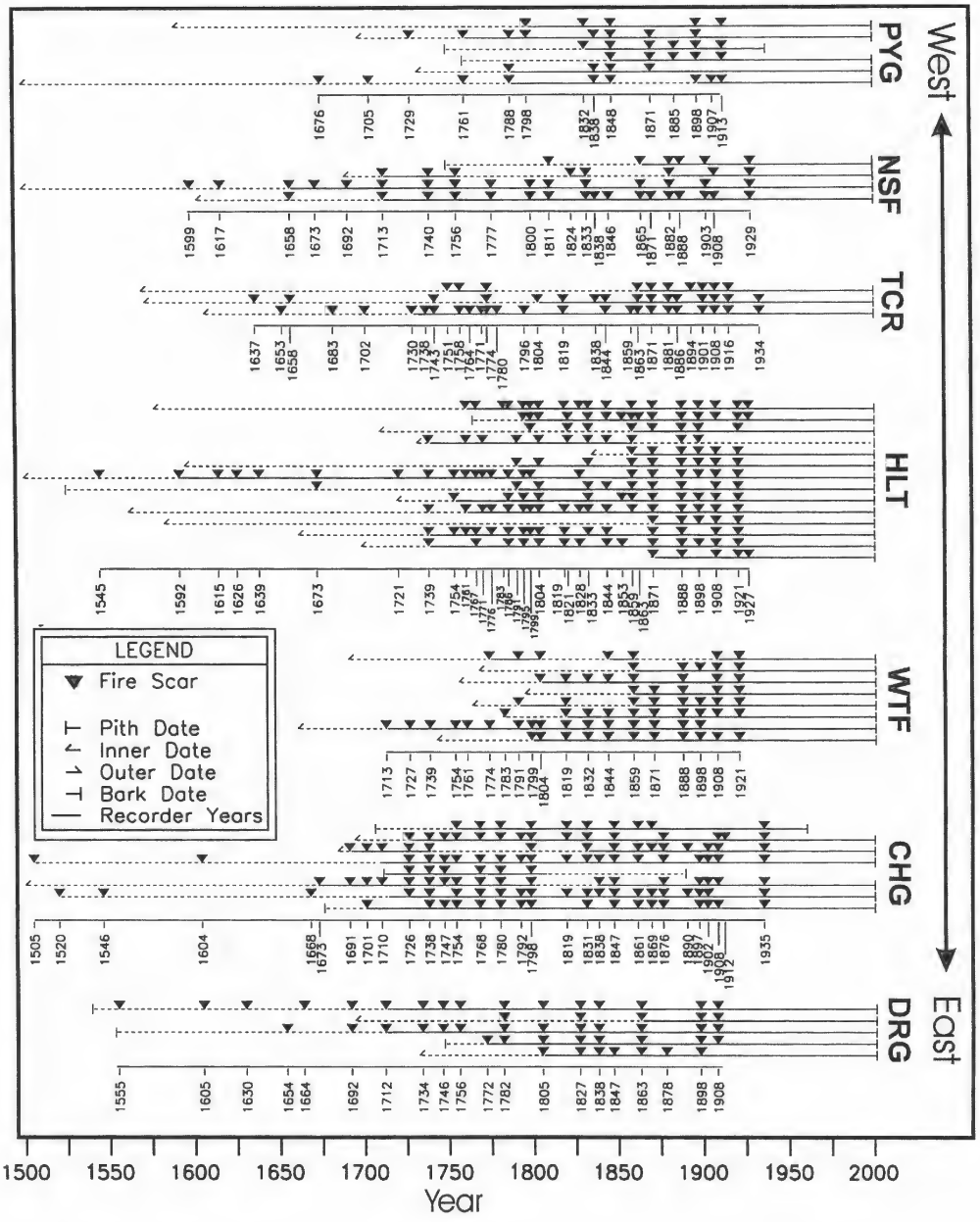


Figure 3. Fire chronologies for Jackson Demonstration State Forest sites. All samples are from coast redwood. Time spans of individual trees are represented by horizontal lines with inverted triangles marking dates of fire scars. Pith or bark dates refer to pith or bark present on cross sections while inside or outside rings refer to cross sections with unknown numbers of rings to pith or bark. Inside dates on several trees extend earlier than 1500. Dashed segments on trees are decayed segments where fire scars are likely missing from the fire-scar record. These segments were not used to calculate point fire frequencies in Table 3.

predictable reason (i.e., not driven by climatic stress) (Fritz and Averill 1924, Fritz 1940) which further complicated compilation of complete ring series within and between trees. For these reasons, we do not consider fire dates reported in Figure 3 to be absolute dates. However, tree-ring and fire-scar dates on most trees in four sites (WTF, NSF, HLT, and CHG) were consistent back to a regionally narrow ring at 1829, and we have greater confidence in dating of fires for this period. In addition, we were able to cross-match timing of fire scars back to the early 1700s in all sites, and fire dates reported in Figure 3 are likely not far off from true dates, if at all. Several fire dates (e.g., 1754, 1819, 1871, 1908) were recorded synchronously across multiple stands (Figure 3), and we have some confidence that these represent larger-scale fires that burned across the JDSF landscape.

No fire scars were recorded in any stand after the middle 1930s (Figure 3). Fire frequency through time appears to have been relatively uniform in most stands, with no major changes in fire frequency through periods of adequate sample depth (i.e., numbers of trees per year) in each chronology. The longest intervals in most chronologies were recorded during the early nineteenth century (Figure 3).

Where fire-scar position within ring series could be determined, fire scars occurred almost exclusively late in the growing season or as dormant season scars between two rings (Table 2). The majority of fires likely occurred during the period from late August to late fall (October to November).

## Fire Frequency Along the Ocean-Inland Gradient

Pre-20th century fire frequency was generally high in all stands, with composite MFIs ranging from 6 to ~ 20 yr depending on site location and period analyzed (Table 3). The longest mean intervals were recorded in the westernmost stand (PYG) and several of the centrally located sites recorded some of the shortest (TCR, HLT). WMPIs are slightly lower than MFIs reflecting positive skew in interval distributions (Grissino-Mayer 1999). Fire-interval distributions tend to be positively skewed and WMPI is argued to be a more robust estimator of central tendency in interval data (Grissino-Mayer 1999). Composite fire frequencies were not significantly related to the ocean-inland gradient in regression analysis. Although there was a tendency for composite frequencies to decrease from west to east (Table 3), this decrease is likely related to the number of trees included in composite fire chronologies which tended to be greater in the more eastern stands (Table 1). Greater number of trees in a composite chronology will tend to include more fires if average fire size was less than the area from which trees were collected (Brown and Swetnam 1994). Furthermore, it is possible that not all fires that burn at the base of an individual tree are recorded as scars and fire scars may be lost from a record by erosion or burning in later fires. Censoring of fire-scar records on individual trees also will result in higher composite fire frequencies with greater number of trees used to calculate composite fire intervals.

TABLE 2. Fire-scar positions in annual rings and probable season of occurrence (fire-scar positions after Dieterich and Swetnam 1984), based on 544 total fire scars.

| Fire-scar position | No. of scars | % of total scars[1] | Probable season of occurrence |
|---|---|---|---|
| Dormant | 217 | 52 | After growth ended; September to late fall |
| Latewood | 164 | 39 | In the latewood band; mid-August to September |
| Late-earlywood | 20 | 5 | Latter third of the earlywood; July to August |
| Middle-earlywood | 15 | 4 | Middle third of the earlywood; June to July |
| Early-earlywood | 0 | 0 | Early-third of earlywood; April to May |
| Unknown | 128 | — | Fire-scar position within ring could not be assessed |

[1] Excluding unknown scars

TABLE 3. Fire frequencies in coast redwood stands at Jackson Demonstration State Forest.

| Site | Period analyzed | Intervals per stand: MFI ± 1 SD (yr) | WMPI (yr) | Range (yr) | Intervals per tree: No. of trees | MFI ± 1 SD (yr) |
|---|---|---|---|---|---|---|
| PYG | 1700s | – | – | – | – | – |
| | 1750 - 1850 | 17.4 ± 12.3 | 15.8 | 6 - 34 | 5 | 24.5 ± 5.9 |
| | 1800s | 13.2 ± 6.3 | 12.9 | 6 - 23 | 6 | 18.8 ± 7.7 |
| NSF | 1700s | 21.8 ± 4.6 | 22.1 | 16 - 27 | 3 | 21.6 ± 0.1 |
| | 1750 - 1850 | 12.9 ± 6.7 | 12.4 | 5 - 23 | 3 | 14.4 ± 5.1 |
| | 1800s | 9.8 ± 4.4 | 9.6 | 5 - 19 | 4 | 13.0 ± 5.1 |
| TCR | 1700s | 9.4 ± 7.4 | 8.3 | 3 - 28 | 2 | 9.9 ± 2.3 |
| | 1750 - 1850 | 9.3 ± 5.3 | 8.8 | 3 - 19 | 3 | 12.4 ± 0.9 |
| | 1800s | 10.0 ± 5.2 | 9.6 | 4 - 19 | 3 | 11.1 ± 0.7 |
| HLT | 1700s | 7.1 ± 4.9 | 6.5 | 3 - 18 | 8 | 11.6 ± 6.2 |
| | 1750 - 1850 | 6.0 ± 3.3 | 5.7 | 2 - 15 | 10 | 13.0 ± 4.9 |
| | 1800s | 8.6 ± 4.6 | 8.1 | 2 - 17 | 14 | 14.5 ± 2.6 |
| WTF | 1700s | – | – | – | 2 | 14.7 ± 3.3 |
| | 1750 - 1850 | 10.0 ± 3.4 | 10.1 | 5 - 15 | 5 | 12.7 ± 1.5 |
| | 1800s | 13.4 ± 2.4 | 13.6 | 10 - 17 | 8 | 14.9 ± 2.3 |
| CHG | 1700s | 10.8 ± 3.3 | 10.9 | 6 - 16 | 8 | 12.2 ± 2.0 |
| | 1750 -1850 | 11.6 ± 4.7 | 11.5 | 6 - 21 | 8 | 13.7 ± 2.0 |
| | 1800s | 9.8 ± 3.1 | 9.8 | 7 - 14 | 7 | 14.1 ± 3.7 |
| DRG | 1700s | 14.0 ± 5.1 | 14.0 | 10 - 22 | 3 | 15.0 ± 4.3 |
| | 1750 - 1850 | 15.2 ± 6.2 | 15.1 | 9 - 23 | 4 | 17.9 ± 3.2 |
| | 1800s | 15.5 ± 5.0 | 15.6 | 9 - 22 | 5 | 24.1 ± 7.0 |

Point fire frequencies averaged within individual trees before averaging within sites confirm that fire frequency did not vary significantly across the ocean to inland gradient (Table 3). There is consistency in fire frequencies recorded on individual trees, with most trees recording interval ranges from around 10 to 20 yr depending on site and period analyzed. Although, again, there was a tendency for the western stands to have recorded slightly longer intervals than those in the east, this trend was not significant in regression analysis.

## Discussion

### Fire History on the Mendocino Coast

Surface fires were frequent disturbances in coast redwood forests of the Mendocino Coast prior to the early 20th century (Figure 3). Long sequences of fire scars recorded on individual trees were rare but present in all old-growth stands we examined. As stated in the methods, because of the random nature of preservation and locations of these stands, we believe that reconstructed patterns of episodic surface fires represent the typical fire regime in this area. Although we did not collect tree-origin data from the stands we sampled, we do not believe that large portions of this area burned in past catastrophic fires over the period covered by fire-scar records, although mixed-severity burning (i.e., containing some component of overstory mortality) likely occurred during some fires across limited areas. Frequent surface fires, by themselves, imply that fuel buildup and formation of ladder fuels needed for fire to burn catastrophically were less likely to have occurred than if intervals between fires were longer (Keane et al. 1990). We were unable to reconstruct fire history in any of the cut-over areas because of a lack of adequate preservation of fire-scar records. Our experience is that processes of decay and erosion have removed fire-scar records from these areas, rather than that the records were never there originally. Coast redwood trees appear to be more susceptible to burning or decay of scarred surfaces, likely as a result of less woundwood formation on fire scar margins as part of the compartmentilization process in the wound area (Figure 4; Smith and Sutherland 2001), in contrast to pines or other

Figure 4. Image of fire-scar sequence on tree TCR-6. Fire scars are marked by black arrows. Note wood decay on outside margins of fire-scar sequences. In coast redwood, compartmentilization through woundwood formation in the injury areas (Smith and Sutherland 2001) tends to stop where fire scars end in the ring series, whereas in other species (e.g., pines, giant sequoia) woundwood formation occurs continuously to the outside of wood growth. More continuous woundwood formation in pines and other species results in less decay of scarred surfaces and thus better preservation of fire-scar sequences through time.

species in which well-preserved fire-scar sequences are commonly used to reconstruct fire history.

Fire frequencies that we reconstructed in stands and on individual trees (Table 3) are similar to fire frequencies recorded in many lower-elevation forests of the western United States, including ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests of the Southwest (Swetnam and Baisan 1996, Brown et al. 2001) and giant sequoia (*Sequoiadendron giganteum*) and mixed-conifer forests of the Sierra Nevada (Swetnam 1993, Beaty and Taylor 2001). Fire frequencies in Table 3 also are comparable to those found in mesic coastal Douglas-fir forests at Olympic National Park well to the north of the Mendocino Coast (Wetzel and Fonda 2000) and strengthen our argument that surface fires are not only restricted to dryer inland forests. As in virtually all fire histories reconstructed from forests throughout western North America, fires ceased entirely during recent decades as a result of land use changes and fire suppression (Figure 3). On the Mendocino Coast, active fire suppression began after the Comptche Fire in September 1931, burned ~12,150 ha of forest southeast of JDSF. Before this date, wildfires were rarely suppressed unless they threatened homes. During the early Euro-American settlement era (after ca. 1850), ranchers and loggers routinely set fires to increase grazing area and to reduce slash before harvesting of logs. After the Comptche Fire, the California Department of Forestry and Fire Protection (CDF) established fire stations that initiated the period of total fire exclusion that continues to the present (Figure 3).

Coast redwood occurs in coastal mountain ranges that receive moisture inputs from cool summer fog during otherwise dry summer months (Roy 1966, Dawson 1998). Fog-shrouded coastal sites would not, at first glance, appear to be areas able to support frequent or widespread surface fires. However, understory fuels typically cure after summer fogs dissipate during the later summer or fall and before winter rains begin (Arno and Alison-Bunnell 2002), which is the period during which most fires occurred in the historical record (Table 2). Although inland stands are warmer with a greater range of temperature variations (Figure 2), fire frequency did not vary significantly along the ocean-inland gradient (Table 3), undoubtedly as a result of other site factors not accounted for by the gradient we tested. Fire occurrence and spatial patterning are highly variable processes, driven by multiple spatial and temporal factors that cannot always be accounted for or predicted. We found fewer well-preserved pre-settlement fire-scar records in stands close to the coast, and most of our data are from what should be considered as intermediate to dry inland stands (Veirs 1982). Forests along the coast were harvested earliest during the early settlement period (Wurm 1986) and presumably experienced more burning - and, thus, greater loss of fire-scar evidence - after trees were cut in the early logging era. The one coastal stand in which we were able to reconstruct pre-settlement fires, PYG, tended to have longer intervals than more inland sites (Table 3). However, all stands, regardless of their location, recorded higher fire frequencies than those hypothesized by Veirs (1980, 1982).

## Implications of the Fire History for Management of Old-Growth Coast Redwood Forests

Loss of surface fires from coast redwood forests has led to changes in associated ecosystem patterns and processes that are analogous to those in ponderosa pine and other low-elevation forests of the western North America (Covington et al. 1994). Frequent surface fires promote open, low-density stand structure by killing a majority of tree regeneration before it has a chance to reach canopy status. Fire-intolerant species, such as grand fir, western hemlock, and hardwoods, would have had less opportunity to establish between fires and likely were not as abundant in pre-fire exclusion forests as they are today. Biomass of shrubs also would have been reduced because of recurrent mortality during episodic burns. Duff and woody litter would have been reduced, and diversity and biomass of grass and herbaceous vegetation likely were correspondingly greater (Covington et al. 1994). Increases in fuel loads, tree density, canopy coverage, and formation of ladder fuels result in feedbacks to the fire regime, with the result that crown fires replace surface fires as the dominant fire behavior when fires occur. Although fire exclusion on the Mendocino Coast occurred later in the 20th century than many other low elevation forests in North America, coast redwood forests are often nearly twice as productive as pine or mixed-conifer forests of the central mountains or Sierra Nevada in California. Because of higher productivity in these relatively warm, wet coastal forests, changes in community

composition and fuels structure may be as pronounced as in other forests that experienced earlier loss of surface fire regimes.

The probable role of Native-Americans in fire ignitions leads to questions concerning the appropriate approach to management of coast redwood ecosystems in this area. In the absence of human ignitions, it is likely that fires would not have been as common, and historical forest composition and structure may have been quite different under such altered fire regimes. Historical variability in fire regimes reconstructed by this study does not imply that we are documenting a natural range of variability (i.e., driven by primarily natural processes). Rather, we document the fire regime that was dominant for the few centuries before fire suppression and other ubiquitous land use impacts brought by rapid human population increases that accompanied Euro-American settlement. Historical data are meant to provide restoration ecologists and land managers with descriptions of ecosystem conditions over long time scales, regardless of whether they were influenced by human or natural factors (Landres et al. 1999). How these data are used in management decisions is as much a societal as it is an ecological question. Do we attempt to restore these forests to historical conditions, or let them return naturally to a fire regime that would have likely been present in the absence of Native American influence?

What is clear from this study is that recent assessments of historical fire regimes in coast redwood forests (Sawyer et al. 2000a) have, for the most part, underestimated the frequency and probable role of surface fires in at least some coast redwood forests over the past several centuries. In our experience, we found fire-scar records to be rare because of poor preservation. Where fire-scar records have been compiled, fire histories have documented that many coast redwood forests are not burning today nearly as often as they did in the past (Finney 1990; Finney and Martin 1989, 1992; Brown and Swetnam 1994; Brown et al. 1999). Recognition of changes caused by loss of surface fires has resulted in efforts to restore historical processes in many low-elevation forests throughout western North America (Landres et al. 1999). The fire history reconstructed by this study provides both guidelines and justification for ecological restoration efforts in coast redwood forests of this region.

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## Literature Cited

Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C.

Arno, S. F., and S. Allison-Bunnell. 2002. Flames in Our Forest: Disaster or Renewal? Island Press, Washington, D.C.

Boyd, R. (editor). 1999. Indians, Fire, and the Land in the Pacific Northwest. Oregon State University Press, Corvalis, Oregon.

Beaty, R. M., and A. H. Taylor. 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, southern Cascades, California, USA. Journal of Biogeography 28:955-966.

Brown, P. M., M. W. Kaye, D. Buckley. 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, California. Northwest Science 73:205-216.

Brown, P. M., M. W. Kaye, L. Huckaby, and C. Baisan. 2001. Fire history along environmental gradients in the Sacramento Mountains, New Mexico: Influences of local patterns and regional processes. Écoscience 8:115-126.

Brown, P. M., and T. W. Swetnam. 1994. A cross-dated fire history from a stand of coast redwood near Redwood National Park, California. Canadian Journal of Forest Research 24:21-31.

Cooper, D. W. 1965. The coast redwood and its ecology. University of California Agricultural Extension Service, Berkeley, California.

Covington, W. W., R. L. Everett, R. Steele, L. L. Irwin, T. A. Daer, and A. N. D. Auclair. 1994. Historical and anticipated changes in forest ecosystems in the inland west of the United States. Journal of Sustainable Forestry 2:13-63.

Dawson, T. E. 1998. Fog in the California redwood forest: Ecosystem inputs and use by plants. Oecologia 117:476-485.

Dieterich, J.H., and T.W. Swetnam. 1984. Dendrochronology of a fire-scarred ponderosa pine. Forest Science 30:238-247.

Finney, M. A. 1990. Fire history from the redwood forests of Bolinas Ridge and Kent Lake Basin in the Marin Municipal Water District. *In* Vegetation and Fire Management Baseline Studies: The Marin Municipal Water District and the Marin County Open Space District (Northridge Lands), Marin County, California. Unpublished report on file at the Marin Municipal Water District.

Finney, M. A., and R. E. Martin. 1989. Fire history in a *Sequoia sempervirens* forest at Salt Point State Park, California. Canadian Journal of Forest Research 19:1451-1457.

Finney, M. A., and R. E. Martin. 1992. Short fire intervals recorded by redwoods at Annadel State Park, California. Madroño 39:251-262.

Fritz, E. 1931. The role of fire in the redwood region. Journal of Forestry 29:939-950.

Fritz. E. 1940. Problems in dating rings of California coast redwood. Tree-Ring Bulletin 6:19-21.

Fritz. E., and J. L. Averill. 1924. Discontinuous growth rings in California redwood. Journal of Forestry 22:31-38.

Grissino-Mayer, H. D. 1999. Modeling fire interval data from the American Southwest with the Weibull distribution. International Journal of Wildland Fire 9:37-50.

Grissino-Mayer, H. D. 2001. FHX2 - software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Research 57:115-124.

Henry, N. 1998. Overview of the Caspar Creek watershed study. Pages 1-10 *In* R. R. Ziemer (technical coordinator), Proceedings of the Conference on Coastal Watersheds: The Caspar Creek Story. USDA Forest Service General Technical Report PSW-GTR-168. Pacific Southwest Research Station, Albany, California.

Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measuring. Tree-Ring Bulletin 43:69-78.

Jacobs, D. F., D. W. Cole, and J. R. McBride. 1985. Fire history and perpetuation of natural coast redwood ecosystems. Journal of Forestry 83:494-497.

Keane, R. E., S. F. Arno, and J. K. Brown. 1990. Simulating cumulative fire effects in ponderosa pine/Douglas-fir forests. Ecology 71:189-203.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of natural variability concepts in managing ecological systems. Ecological Applications 9:1179-1188.

Lewis, H. T. 1973. Patterns of Indian Burning in California: Ecology and Ethnohistory. Ballena Press Anthropological Paper No. 1, Ramona, California.

Morgan, P, G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. Historical range of variability: a useful tool for evaluating ecosystem change. Journal of Sustainable Forestry 2:87-111.

National Geophysical Data Center. 2002. The International Tree-Ring Data Bank. Available online at http://www.ngdc.noaa.gov/paleo/treering.html.

Program for Climate, Ecosystems, and Fire Applications. 2002. Automated Lightning Detection System climatology. Available online at http://www.cefa.dri.edu/Cefa_Products/ Lightning/alds_index.htm.

Roy, D. F. 1966. Silvical characteristics of redwood. USDA Forest Service Research Paper PSW-28. Pacific Southwest Research Station, Berkeley, California.

Sawyer, J. O., S. C. Sillett, W. J. Libby, T. E. Dawson, J. H. Popenoe, D. L. Largent, R. Van Pelt, S. D. Veirs, Jr., R. F. Noss, D. A. Thornburgh, and P. Del Tredici. 2000a. Redwood trees, communities, and ecosystems: A closer look. Pages 81-118 *In* R.F. Noss (editor), The Redwood Forest. Island Press, Washington, D. C.

Sawyer, J. O., S. C. Sillett, J. H. Popenoe, A. LaBanca, T. Sholars, D. L. Largent, F. Euphrat, R. F. Noss, and R. Van Pelt. 2000b. Characteristics of redwood forests. Pages 39-80 *In* R.F. Noss (editor), The Redwood Forest. Island Press, Washington, D. C.

Schulman, E. 1940. Climatic chronology in some coast redwoods. Tree-Ring Bulletin 5:22-23.

Smith, K. T., and E. K. Sutherland. 2001. Terminology and biology of fire scars in selected central hardwoods. Tree-Ring Research 57:141-147.

Stokes, M. A., and T. L. Smiley. 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, Illinois.

Stone, E. C., R. F. Grah, and P. J. Zinke. 1972. Preservation of the primeval redwoods in the Redwood National Park, Part I. American Forests 78(4):50-56.

Stuart, J. D. 1987. Fire history of an old-growth *Sequoia sempervirens* (Taxodiaceae) forest in Humboldt Redwoods State Park, California. Madroño 34:128-141.

Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885-889.

Swetnam, T. W., and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since 1700. Pages 11-32 *In* C. D. Allen (editor), Fire Effects in Southwestern Forests, Proceedings of the 2nd La Mesa Fire Symposium, March 29-31, 1994, Los Alamos, New Mexico. USDA Forest Service General Technical Report RM-GTR-286. Rocky Mountain Research Station, Fort Collins, Colorado.

Thornburgh, D. A., R. F. Noss, D. P. Angelides, C. M. Olson, F. Euphrat, and H. H. Welsh, Jr. 2000. Managing redwoods. Pages 229-262 *In* R. F. Noss (editor), The Redwood Forest. Island Press, Washington, D. C.

Veirs, S. D. 1980. The influence of fire in coast redwood forests. Pages 93-95 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings of the fire history workshop, October 20-24, 1980, Tucson, Arizona. USDA Forest Service General Technical Report RM-81. Rocky Mountain Research Station, Fort Collins, Colorado.

Veirs, S. D. 1982. Coast redwood forests: Stand dynamics, successsional status, and the role of fire. Pages 119-141 *In* J. E. Means (editor), Forest Succession and Stand Development Research in the Northwest. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Veirs, S. D. 1996. Ecology of the coast redwood. *In* J. LeBlanc (editor), Proceedings of the Conference on coast redwood forest ecology and management. University of California Cooperative Extension Forestry Publication, Humboldt State University, Arcata, California.

Westman, W. E., and R. H. Whittaker. 1975. The pygmy forest region of northern California: Studies on biomass and primary production. Ecological Monographs 63:453-520.

Wetzel, S. A., and R. W. Fonda. 2000. Fire history of Douglas-fir forests in the Morse Creek drainage of Olympic National Park, Washington. Northwest Science 74:263-279.

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*Accepted for publication 30 September 2002*

Wright, H. A., and A. W. Bailey. 1982. Fire Ecology: United States and Canada. John Wiley and Sons, New York, New York.

Wurm, T. 1986. Mallets on the Mendocino Coast. Timber Times, Inc., Hillsboro, Oregon.

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# Western Spruce Budworm Defoliation Effects on Forest Structure and Potential Fire Behavior

## Abstract

Forest composition and structure on the eastern slope of the Cascade Mountains have been influenced by decades of fire exclusion. Multi-layered canopies and high numbers of shade-tolerant true fir trees interact with western spruce budworm to alter forest structure and to affect potential fire behavior and effects. We compared measurements taken in 1992 (early budworm outbreak) and 2000 (late budworm outbreak) from 21 permanent plots located in a late successional reserve south of Mt. Adams in Washington. Canopy closure decreased significantly, from a mean of 78% in 1992 to 43% in 2000, but the coarse woody debris load increased significantly during the same period, from about 40 Mg $ha^{-1}$ to 80 Mg $ha^{-1}$. Tree mortality was mostly in the smaller (<20 cm) diameter classes. Potential surface fire flame lengths increased significantly from 1.4 m in 1992 to 1.9 m in 2000, but changes in torching potential and independent crown fire behavior were not significant. Projections using the First Order Fire Effects Model indicate that a wildfire in conditions similar to those in 2000 would not be of stand replacement severity and would leave 148 trees $ha^{-1}$ and more than 34 $m^2$ $ha^{-1}$ of basal area.

## Introduction

Biological and social concerns about the persistence of species associated with old forests of the U. S. Pacific Northwest helped to create a regional forest reserve network in 1994 (USDA and USDI 1994). These reserves—called late successional reserves (LSR)—are located on federal land throughout the range of the northern spotted owl (*Strix occidentalis caurina*) in Washington, Oregon, and California (Figure 1). One LSR objective is to protect late successional forest from large-scale fire, insect and disease epidemics, and major human impacts (USDA and USDI 1994). Here we evaluate how insect and fire interaction may affect this objective for a LSR in the eastern Washington Cascades physiographic province (Figure 1).

Forest structure and species composition are shaped by disturbance history and, in turn, influence disturbance dynamics. The mid-elevation, mixed-conifer forest on the east slope of the Cascade Mountains has a variable-intensity, mixed-severity fire regime (Agee 1993). Low-intensity surface fires favor dominance by ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), and Douglas-fir (*Pseudotsuga menziesii*), which have thick, fire-resistant bark (Arno et al. 1985, Prance and Prance 1993). Low- or moderate-intensity fires favor seral tree species such as Douglas-fir and western larch, over species like grand fir (*Abies grandis*), which has thinner bark and is thus more easily killed by fire (Agee 1993). Federal fire exclusion policies dating to the early 20th century (Dana and Fairfax 1980) have extended fire-free intervals in western states (Covington et al. 1994), and in the mid-elevation forests on the eastern slope of the Cascade Mountains this has resulted in higher numbers of shade-tolerant, fire-intolerant grand fir (Camp 1999).

Changes in species composition have been accompanied by structural changes in the amount and distribution of foliage and of dead or dying trees. Higher biomass of late successional trees like grand fir (Brookes et al. 1985) and more canopy layers (Brookes et al. 1987) increase forest susceptibility to outbreaks of insects such as the western spruce budworm (*Choristoneura occidentalis*) (Hessburg et al.1994, Swetnam and Lynch 1993, Swetnam et al. 1995). Trees may die if spruce budworm defoliation persists over several years (Edmonds et al. 2000), which contributes dead wood to the structural complexity and ecological function of the forest (McComb and Lindenmayer

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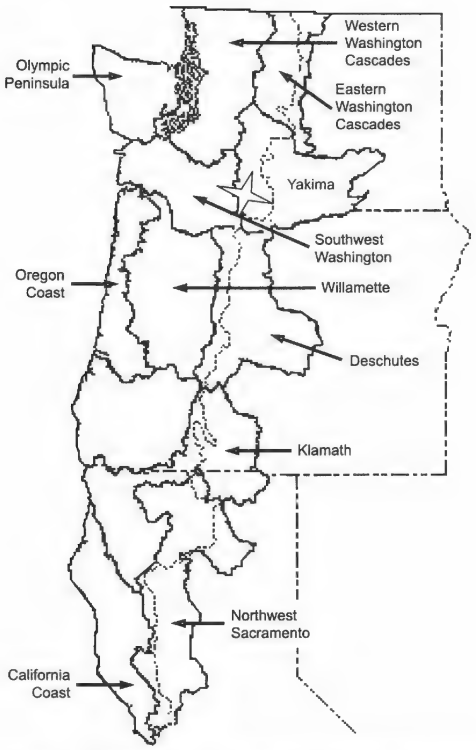


Figure 1. Physiographic provinces within the range of the northern spotted owl (source: FEMAT 1993). Star identifies location of this study.

1999). Tree size and age diversity, canopy foliage distribution, and dead wood are all important components of forest structure (Spies 1998).

Forest structure interacts with fire behavior, which is a function of fuels, weather, and topography (Agee 1996). A fire may move through a forest as a surface fire, an independent crown fire, or some combination thereof (Van Wagner 1977). Intense surface fire may transition into a crown fire through a process called torching, which is a function of the height to live crown and foliar moisture content. Above threshold conditions of fireline intensity defined by these variables, the fire will move into the canopy. Independent crown fire spread is a function of fire rate of spread and the foliar density of the canopy (Scott and Reinhardt 2001).

In late successional reserves, developing or maintaining forest structure that supports species like the spotted owl is a key goal (USDA and USDI 1994). Large trees, downed wood, and dense, multilayered forest canopies are important because these features support owl nesting and foraging activities (Thomas et al. 1990). Spotted owl nest sites on the eastern side of the Cascade Mountains are reported to have a broader array of structural conditions than on the western side (Everett et al.1992), but common elements include closed canopy forests with large Douglas-fir trees, downed wood, and multiple canopy layers (Buchanan et al. 1995, King et al. 1997). Depending on their magnitude and intensity, budworm defoliation and fire might affect these elements of owl habitat in different ways. The spruce budworm modifies forest structure by increasing mortality of defoliated understory trees, by predisposing larger trees to attack by bark beetles (*Dendroctonus* or *Scolytus* spp.), and by altering the amount of canopy foliage (Hadley and Veblen 1993). The duration and frequency of budworm outbreaks have increased with decreasing forest fire frequency in the western states (Anderson et al. 1987). Fire modifies forest structure along a gradient, thinning smaller to larger trees and thin- to thicker-barked species as fireline intensity increases. We investigated the interaction of budworm and fire by measuring how live and dead forest structure is changing in association with budworm defoliation and by simulating how these changes affect potential fire behavior and effects.

## Study Site

Our study site is in south-central Washington state in the Gifford Pinchot National Forest (Hummel et al. 2001) (Figure 1). The approximately 80-ha site covers Smith Butte, a cinder cone related to Mt. Adams that lies 13 km south of the mountain and about 3 km west of the Yakama Indian Reservation. The elevation of Smith Butte ranges from 1120 to 1300 m and slopes, which average 22°, range from 10° to 31°. The volcanic parent materials are covered by coarse-textured, sandy loam soils ranging from 0.15-1.2 m deep (Gifford Pinchot National Forest Soil Resource Inventory 1971). Vegetation varies by aspect and elevation, but generally resembles the grand fir/creeping snowberry/vanillaleaf (*Abies grandis/Symphoricarpos mollis/Achlys triphylla*) or grand fir/big huckleberry (*Abies grandis/Vaccinium membranaceum)* associations described in Franklin and Dyrness (1988) and Topik (1989). Several species

of conifer root pathogens occur in scattered pockets across the study site (Filip 1980). The nearest weather records are from the USDA Forest Service Mt. Adams Ranger Station in Trout Lake, Washington, which is located about 10 km southwest and 600 m lower than Smith Butte. Trout Lake receives about 116 cm of annual precipitation, and snow generally covers Smith Butte from November to April.

Current forest conditions on Smith Butte are atypical for the area because, although Douglas-fir, ponderosa pine, and western larch have been harvested from surrounding forest, the butte has not been logged. A map from the 1940s shows the forest types on Smith Butte by aspect: mature Douglas-fir on the west flank, large-pole ponderosa pine on the south flank, and mixed conifer on the east flank. These forest types, which the map illustrates but does not explicitly define, were roughly equal in size (20-28 ha) (Bright 1941). Current conditions are a legacy of these relict forest types, and the butte is, therefore, a type of refugium (Camp et al. 1997) where research opportunities abound. Indeed, Smith Butte was considered for inclusion in a network of Research Natural Areas (RNA) (Franklin et al. 1972) and a grid of 21 sample points was established in 1992. Although vegetation conditions at each point were measured and the center location permanently marked, Smith Butte never became a designated RNA. Efforts have been revived to obtain RNA status, in part because a meadow on top of the butte provides habitat for the mardon skipper (*Polites mardon*), a butterfly listed as endangered by the state of Washington (Potter et al. 1999).

In 1994, Smith Butte was included in the 6000 ha Gotchen LSR and became subject to the Gifford Pinchot National Forest objectives for the reserve (USDA Forest Service 1997). Also in 1994, annual aerial detection surveys began recording a budworm outbreak in the Gotchen LSR. Budworm had been increasing from endemic levels since the late 1980s, and by 1992 defoliation was apparent from the ground (Jim White, USDA Forest Service, personal communication 2000). Annual defoliation has been documented since 1992 (Willhite 1999). Since 1999 annual counts of budworm larvae and adult moths indicate a sharp decline for populations in the vicinity of Smith Butte (Beth Willhite, USDA Forest Service, personal communication 2001).

Smith Butte is adjacent to a spotted owl nest site that has been monitored for a decade. Although the nest site previously provided suitable habitat, by 2001 successful owl reproduction at had not been documented for at least 3 yr (Mendez-Treneman 2001). This decline occurred simultaneously with the ongoing budworm defoliation and inspired our research questions.

### Objectives

Our objectives were to investigate how spruce budworm defoliation on Smith Butte has altered forest structure and how the changes might influence fire behavior and effects. It is difficult to predict the course of the current budworm outbreak, but for this study we consider 1992 to be early in the outbreak and 2000 to be late. We tested two null hypotheses relative to spotted owl habitat elements: 1) canopy closure has not changed and 2) the basal area of large trees has not changed. We tested five null hypotheses relative to fire behavior and effects: 1) coarse woody debris levels have not changed, 2) potential surface fire behavior has not changed, 3) torching potential has not changed, 4) independent crown fire potential has not changed and 5) potential tree density and basal area losses to wildfire have not changed.

## Methods

The 21 sample points installed on Smith Butte in 1992 were remeasured in 2000. We recorded the location, slope, aspect, and plant association for each point. Each sample point consisted of three nested plots and a fuel transect. The largest plot had a variable radius, based on a 40 (English unit) basal area factor (BAF) prism (Bell and Dilworth 1988). Inside this variable radius plot were two fixed plots: one 0.02 ha and the other 0.008 ha. Each plot shared the same center stake. The 100 m fuel transect extended from the center stake in the direction of the next sample point. Supplemental fuels data on fuelbed depth and aboveground biomass were collected in 2001 using the estimation procedures in NEWMDL (Burgan and Rothermel 1984), a program that creates a fuel model suitable for fire behavior prediction from field-collected data. Data from 1992 and 2000 were compared using various statistical tests and software packages. Data from the variable radius plot were used to test hypotheses about changes in canopy closure and conifer

basal area between 1992 and 2000, whereas data from the fixed plots and the fuel transect were used to test hypotheses about changes in fire behavior for the same period. Details about the methods and analyses are provided below.

### Trees and Snags

In the variable radius plot, data were collected on canopy closure and on all trees and snags larger than 12.5 cm dbh (diameter at breast height or 1.3 m). Canopy closure was estimated using a spherical densiometer (in 1992) and a moosehorn densitometer (in 2000). Densiometers may overestimate actual cover in mature conifer stands by 3-9% compared to densitometers (Ganey and Block 1994). Two canopy closure measurements were made, each 3.6 m from the center (adjusted for slope), north and south of the plot center stake. The average of these two measurements is the point value. Sample trees and snags were selected using standard variable plot sampling methods (Bell and Dilworth 1988). An average of 6-8 trees per point resulted from using the 40 BAF prism. For each sample tree species, status (live or dead), diameter and height were measured or estimated. For each sample snag, the measured attributes included species, diameter, and height.

### Shrubs, Herbs, and Tree Regeneration

In the fixed-radius plots, all shrub and herb species were recorded, together with an estimate of cover to the nearest 10% and a tally of conifer regeneration. Estimates of shrub and herb cover were made by using the comparison charts for visual estimation of foliage cover by Terry et al. (1955) as adopted by the USDA Forest Service Pacific Northwest Region 6 Area Ecology Program (Topik 1989).

### Fuels

Along the 100 m transect, fuels data were collected based on Brown (1974). Fuels are the dead twigs, branches, and boles of trees and shrubs that have fallen and lie on the ground. Calipers were used to measure all coarse woody debris (> 7.6 cm in diameter) within 2 m of the ground over the entire transect. Smaller fuels and duff depth were sampled on three 2.7 m segments. The first interval began at 40 m from the center stake, the second at 60 m, and the third at 80 m. Data on fine fuels were collected in each sampling segment. The 1-hour fuel load (0-0.62 cm diameter) was tallied over the first 0.91 m of the segment, the 10-hour fuel load (0.63-2.54 cm diameter) was tallied over the first 1.8 m, and the 100-hour fuel load (2.55-7.62 cm diameter) was tallied over the entire 2.7 m.

### Surface Fire Behavior

Two components of surface fire behavior (fuelbed depth and aboveground live biomass) were not directly measured in either 1992 or 2000, so we estimated them by using shrub and herb cover data collected in 2000 together with biomass estimates in 2001. We assume biomass changed minimally between 2000 and 2001. For 1992 biomass values, the 2000 cover data and the 2001 biomass estimates were used to develop regression equations for herb and shrub loadings. These equations are:

$$\text{HerbLoad (t/ac)} = 0.08181 \text{ Ln (Herb Cover [\%])} \quad r^2 = 0.63$$
$$\text{ShrubLoad (t/ac)} = 0.11170 \text{ Ln [Shrub Cover [\%])} \quad r^2 = 0.36$$

We used these relationships to estimate 1992 herb and shrub loads from the 1992 cover data. Based on our estimates, we assigned the fuelbed depth of the Northern Forest Fire Laboratory (NFFL) Model 10 (Albini 1976) to 1992. For 2000, we used our estimates of fuelbed depth from 2001.

## Analysis

### Habitat Elements

Changes in canopy closure, the basal area of large conifers, and down wood between 1992 and 2000 were evaluated by subtracting the 1992 estimates of canopy closure, basal area by size class, sound coarse woody debris, rotten coarse woody debris, and total coarse woody debris from the 2000 estimates for each plot.

#### *Canopy Closure*

A paired t-test was used to compute the mean difference in canopy closure between 1992 and 2000 ($P = 0.05$ for all analyses). Due to missing values, 13 paired plots were available for analysis (Table 1).

#### *Basal Area*

Basal area per tree was computed from measured diameters and the values summed into 12.7 cm diameter classes for all live grand fir and Douglas-

TABLE 1. Difference in canopy closure (%) between 1992 and 2000 for points on Smith Butte.

| Point number | 1992 | 2000 | Difference |
|---|---|---|---|
| 1 | 70 | 75 | 5 |
| 2 | 60 | 33 | -27 |
| 3 | 80 | 32 | -48 |
| 5 | 90 | 26 | -64 |
| 9 | 80 | 30 | -50 |
| 13 | 60 | 42 | -18 |
| 14 | 70 | 27 | -43 |
| 15 | 90 | 60 | -30 |
| 16 | 90 | 16 | -74 |
| 17 | 70 | 57 | -13 |
| 19 | 80 | 47 | -33 |
| 20 | 80 | 62 | -18 |
| 21 | 90 | 50 | -40 |

fir trees. The difference in means between 1992 and 2000 of diameter classes larger than 63.5 cm dbh was compared using a one sample, two-sided paired t-test for the 16 plots on which large trees existed.

## Fuels and Fire Behavior

Changes in fire and woody debris parameters between 1992 and 2000 were evaluated by subtracting the 1992 values for surface fire flame length, critical torching flame length, actual flame length, critical canopy bulk density, actual canopy bulk density, sound coarse woody debris, rotten coarse woody debris, and total coarse woody debris from the 2000 values. One-sample, two-sided t-tests with the null hypothesis that the difference was zero were performed on each parameter.

Surface fire behavior predictions were made through the TSTMDL program of BEHAVE (Burgan and Rothermel 1984). Fuel models for each plot were developed by altering the NFFL Model 10 (Albini 1976) with new fuel loads and fuel depths. Slope was entered as the percent slope normal to the contour at each plot location. Weather was estimated from FireFamily (Bradshaw and McCormick 2000) summaries of historic fire weather at the nearest weather station (Trout Lake) at the 70-percentile and 95-percentile fire weather (Table 2). Wind speeds were adjusted down by a factor of 0.9 in stands with high canopy cover (>70%) with lower adjustment factors in more open stands with lower canopy cover (Rothermel 1983).

TABLE 2. Fire weather for Trout Lake.

| Variable | 70th Percentile | 95th Percentile |
|---|---|---|
| 1-hr fuel moisture (%) | 6.85 | 4.01 |
| 10-hr fuel moisture (%) | 10.59 | 6.00 |
| 100-hr fuel moisture (% | 12.95 | 8.71 |
| Herbaceous fuel moisture (%) | 90.77 | 55.01 |
| Woody fuel moisture (%) | 120.61 | 92.95 |
| 6.1 m wind speed (km $hr^{-1}$) | 14.5 | 22.5 |

Torching and independent crown fire behaviors were assessed by the technique of Van Wagner (1977). We enabled torching if the predicted fireline intensity from BEHAVE (95 percentile) exceeded the critical fireline intensity defined by Van Wagner (1977):

$$I_o = \{0.01BLC(460 + [26FMC])\}^{3/2}$$

Where $I_o$ = critical surface fireline intensity (kW $m^{-1}$)
BLC = base to the live crown (m)
FMC = foliar moisture content (percent)

Foliar moisture was treated as a constant 90% in these analyses, based on 95-percentile moisture of woody plants derived from local weather records. Base to the live crown was estimated from individual plot tree data in 1992 and 2000 as evaluated by the Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS) (Beukema et al. 2000). Fireline intensity can be scaled to flame length; our results are expressed in terms of surface fire flame length and critical flame length.

Independent crown fire activity was assessed by comparing critical levels of canopy bulk density ($CBD_c$) to actual levels defined by FFE-FVS ($CBD_a$) (Beukema et al. 2000). We use canopy bulk density instead of crown bulk density (Scott and Reinhardt 2001), but in previous literature the two terms are interchangeable. Critical levels were defined by comparing actual to critical canopy bulk densities (Van Wagner 1977, Williamson 1999). Independent crown fire behavior depends on maintaining a minimum level of heat flux into the unburned fuel ahead of the fire. The heat flux is a function of fire rate of spread, the bulk density of the crown, and heat of ignition:

$$E = R(CBD)h$$

Where E = net horizontal heat flux (kW $m^{-1}$)
R = rate of spread (m $sec^{-1}$)
CBD = canopy bulk density
h = heat of ignition (kJ $kg^{-1}$)

The equation can be expressed in terms of mass flow rate:

$$S = R(CBD) = E/h$$

Where $S$ = mass flow rate (kg $m^2$ $sec^{-1}$)

Van Wagner (1977) empirically defined a minimum mass flow rate (S) of 0.05 kg $m^2$ $sec^{-1}$ below which independent crown fire spread was not possible. Therefore, a critical canopy bulk density ($CBD_c$), defined as the canopy bulk density below which independent crown fire spread is unlikely, is:

$$CBD_c = 0.05/R$$

Rates of forward spread (R) were estimated for each plot based on Rothermel (1991). The 95-percentile fire weather was used to estimate surface fire rate of spread on each plot using NFFL Fuel Model 10 (Albini 1976) and a 0.4 adjustment to open windspeed, with that value multiplied by 3.34 to obtain R. The calculated $CBD_c$ then was compared to the $CBD_a$ from the FFE-FVS program to determine whether crown fire should be enabled for that plot.

### Potential Fire Effects

The tree list data from 1992 and 2000, along with the flame lengths from BEHAVE using 95-percentile fire weather, were used as inputs to the First Order Fire Effects Model (FOFEM) (Reinhardt et al. 1997). Absolute and percent change in basal area due to a simulated wildfire in the 1992 forest and the forest in 2000 were calculated from the percentage mortality of each tree list species and size combination on each plot. If torching or independent crown fire were predicted for a plot, the post fire density and basal area was set to zero. Basal area and density proportional loss were analyzed through a paired t-test using an arcsin-square root transformation of the proportion.

## Results

### Canopy Closure

We measured a significant decrease in canopy closure between 1992 and 2000 ($P<0.0001$). On average, canopy closure decreased from 78% in 1992 to 43% in 2000 (Table 1). The 95% confidence interval calculated around the mean difference indicates that the change varies from –48 to –22%. This decrease is much greater than possible error due to different sampling methods in the two periods. It likely stems from a combination of defoliation on large trees and mortality of smaller ones. Tree density decline was primarily in the smaller size classes (Figure 2).

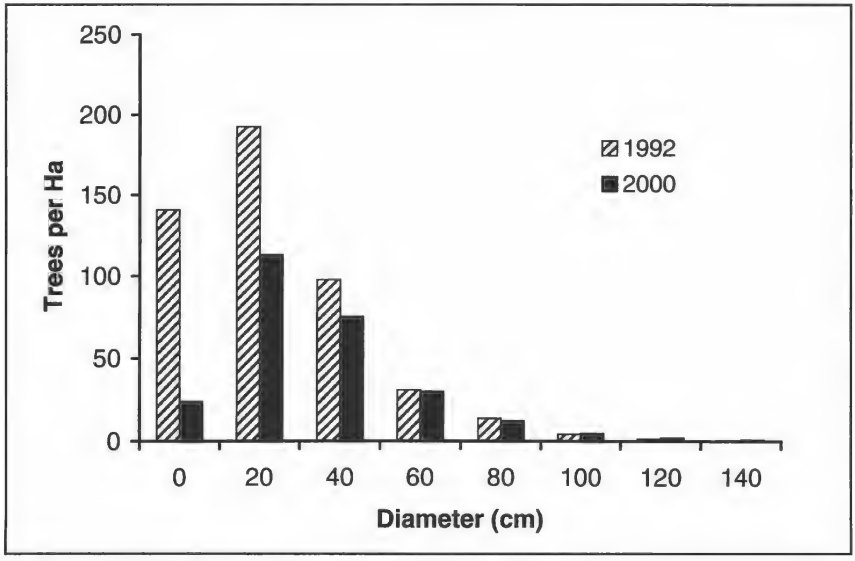


Figure 2. Tree density early (1992) and late (2000) in the western spruce budworm defoliation event.

## Basal Area of Large Trees

No significant difference in the basal area of large Douglas-fir or grand fir trees was found between 1992 and 2000. The mean basal area of large trees (>63.5 cm dbh) was 4.64 $m^2$ $ha^{-1}$ in 1992 compared to 5.05 $m^2$ $ha^{-1}$ in 2000.

## Fuels and Fire Behavior

### *Downed Wood*

The mean downed coarse woody debris load in 1992 was about 40 Mg $ha^{-1}$, about 60% of which was sound (Table 3). By 2000, the load was significantly greater in all categories and fuel bed depth indicates this higher loading was tightly packed. Sound coarse woody debris increased by an average of 14.2 Mg $ha^{-1}$ ($P$ = 0.02), rotten material increased by 24.3 Mg $ha^{-1}$ ($P$ = 0.001), and the total coarse woody debris increased by the sum of these differences (38.5 Mg $ha^{-1}$; $P$ = 0.001). In eight years, the coarse woody debris load nearly doubled.

TABLE 3. Coarse woody debris (Mg $ha^{-1}$) at Smith Butte in 1992 and 2000.

| Category | 1992 | 2000 | Difference |
|---|---|---|---|
| Sound | 23.15 | 37.35 | 14.21 |
| Rotten | 17.67 | 41.97 | 24.30 |
| Total | 40.82 | 79.32 | 38.50 |

### *Surface Fire Behavior*

Predicted surface fire flame lengths significantly increased (Table 4, Figure 3) from 1.4 m in 1992 to 1.9 m in 2000 ($P$ = 0.0003). This was largely a function of increasing fuel load, because topography and weather inputs remained constant. Midflame windspeed increased somewhat because of a more open canopy.

### *Torching and Crown Fire Behavior*

In 1992, four of the 21 plots had torching enabled. Most of the plots did not, however, because of the large difference between the critical flame length needed for torching and the lower actual flame length predictions (Table 4). In 2000, the number of plots where torching was enabled declined to two. None of the four plots in which torching was enabled in 1992 had torching enabled

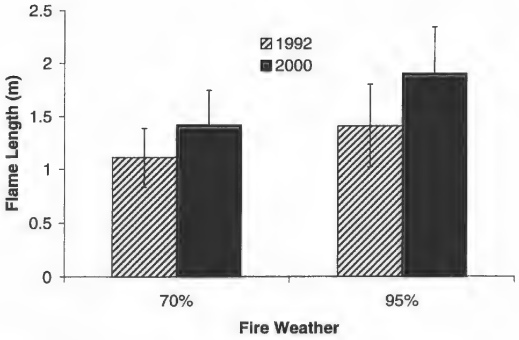


Figure 3. Average surface fire flame lengths across 21 Smith Butte plots in 1992 and 2000. Error bars indicate one standard deviation.

TABLE 4. Fire behavior and crown character estimates for 1992 and 2000.

| Variable | 1992 | 2000 | Difference |
|---|---|---|---|
| Flame length (m) | 1.4 | 1.9 | 0.5 |
| Critical flame length (m) | 3.0 | 3.3 | 0.3 |
| Height to live crown (m) | 6.9 | 8.9 | 2.0 |
| Actual canopy bulk density (kg $m^{-3}$) | 0.11 | 0.12 | 0.01 |
| Critical canopy bulk density (kg $m^{-3}$) | 0.19 | 0.19 | 0 |

in 2000. This variable response is supported by statistical analyses, which showed that height to live crown and critical torching flame lengths did not differ significantly between 1992 and 2000. Critical flame lengths decreased on 7 plots, increased on 10 plots, and showed no change on 1 plot.

Crown characteristics that contribute to independent crown fire potential did not change significantly during this time period (Table 4). Actual canopy bulk densities as measured by FFE-FVS did not change significantly between 1992 and 2000, and critical canopy bulk densities remained stable.

## Potential Fire Effects on Forest Structure

Early in the budworm outbreak, a wildfire burning in 95-percentile fire weather would have removed about 22% of the density and 21% of the basal area (Figure 4). Moderate flame lengths (Table 4) and stand dominance by large trees

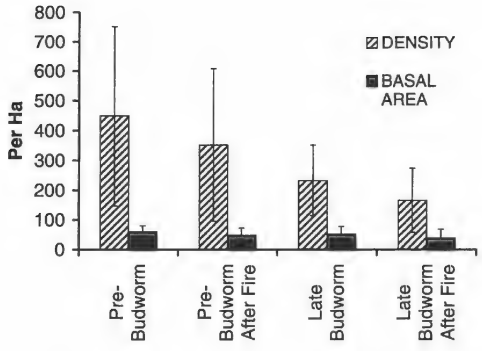


Figure 4. Basal area ($m^2 ha^{-1}$) and density (trees $ha^{-1}$) in the early budworm condition (1992), the early budworm condition if burned by a 95-percentile weather fire, the late budworm condition (2000), and the late budworm condition if burned by a 95-percentile weather fire. Error bars indicate one standard deviation.

contribute to this low predicted loss. Between 1992 and 2000, tree mortality was mostly in the smaller diameter classes (Figure 2) and the residual stand thus maintained a large average diameter. Greater surface fire behavior did not have significant impacts on the proportional loss of density and basal area, which in 2000 averaged 29% and 25% respectively. Absolute density and basal area were larger in 1992 than in 2000, but proportional loss did not differ significantly for either density or basal area between 1992 and 2000. Our FOFEM predictions indicate that a wildfire in conditions similar to those measured in 2000 would leave residual stands on Smith Butte stands with 148 trees $ha^{-1}$ and more than 34 $m^2 ha^{-1}$ of basal area.

## Discussion

Forest structure, including canopy closure and levels of downed wood, has changed significantly on Smith Butte following 8 yr of budworm defoliation. Changes in forest fire behavior resulting from human or natural disturbance can be expressed as changes in surface fire, torching potential, and independent crown fire potential. Our assessment of fire behavior changes on Smith Butte includes all three, with mixed results. Coarse woody debris levels are significantly higher, and this increase in fuels contributes directly to a predicted increase in surface fire flame lengths. In contrast, the effects on torching potential and crown fire behavior were moderated by the pattern of tree mortality.

We expected more extreme flame lengths, given both the large surface fuel loads in 2000 and the significant increase since 1992. Other studies have predicted much greater losses in defoliated stands due to the buildup of fuels from trees killed by budworm (Mutch et al. 1993). Two factors may have moderated our predicted flame lengths. Fuelbed depth is the first moderating factor. During our 2001 site visit, we rarely saw places with fuelbeds deeper than 0.60 m. This means that the high amount of woody debris was tightly packed, and that these compressed fuels created an unfavorable packing ratio. If, in our analysis, we had made the fuels less compressed and thus deepened the fuelbed, fire behavior would have increased, particularly for the 2000 measurements. The second moderating factor was the relatively mild 22.5 km $hr^{-1}$ windspeed at 95-percentile weather, and the reduction factor of 0.9 used for the closed canopy stands. If we had used higher windspeeds typical of weather stations east of our study site, or had used a less conservative windspeed reduction factor of 0.7 or 0.8, fire predictions would have resulted in more intense surface wildfire behavior.

The amount and pattern of tree mortality affected both fire behavior and stand structure, and therefore had complex effects on predicted fire severity. The proportional loss in tree density and basal area after a fire was predicted to be the same for 1992 and 2000, even though there was almost a 50% decrease in tree density late in the budworm event (Figure 4). A substantial density of snags will add to the down coarse woody debris totals over the next decade regardless of whether a fire occurs, and an additional 30% reduction in tree density is predicted if a wildfire burns the area. While coarse woody debris is not a factor in surface fire potential models, intense fires may receive an important contribution of energy from large fuel (Rothermel 1991). This additional fuel could play a role in extending the duration and increasing the severity of fires above what our results predict. In contrast, the response of shrub and herb loads should continue to increase in the more open forest, which can dampen the effect on surface fire behavior (Agee et al. 2000). While it is not clear how fire behavior will change, it is

clear that ongoing tree mortality will continue to affect potential fire severity on Smith Butte.

Although the residual live tree graph (Figure 2) appears similar to what might result from either a mechanical low thinning (Smith 1962) or fire, the effect of the small tree mortality associated with budworm defoliation is different. Mechanical thinning typically removes many stems at once, whereas the mortality on Smith Butte occurred over several years. Instead of being removed, the dead trees are either falling to the ground or remaining as snags. The net effect of a fire would also be less residual coarse woody debris than that associated with budworm defoliation, because fuel existing prior to the budworm outbreak would be consumed, even as new mortality occurred. In both instances, more woody debris results from the small tree mortality associated with budworm defoliation. Our simulations suggest that current debris loads will not result in stand replacement fires, but more surface woody debris will be accruing over time as current snags fall and perhaps more are created.

The structural elements that moderate potential fire severity on Smith Butte, namely large trees that are fire-resistant because of thick bark and tall crowns, are also elements considered important for spotted owl habitat. Immediately following a disturbance, structural elements like canopy closure or basal area per hectare might not be sufficient for spotted owl habitat, but such effects might be short term (decades) rather than long term (centuries). Future effects on owl habitat would be very different if the large trees on Smith Butte did not survive either a wildfire or subsequent insect or pathogen attacks. Increasing levels of large woody debris may benefit owls by improving conditions for key prey species, but the fire risks and hazards associated with such levels are not well understood.

A remeasurement of the Smith Butte plots is planned to assess how continued mortality and fuel inputs affect fire behavior. Since several root pathogens are also present at the site, we cannot be completely certain how much mortality is attributable to budworm, but the remeasurement should help characterize the lag effects of budworm defoliation.

It is important to remember that the conditions on Smith Butte are uncommon in the area. Indeed, forests with large diameter, early-seral, fire resistant tree species are not common in eastern Washington, owing to harvest history (Covington et al. 1994). Our projections suggest that within such relict patches, fire behavior may not result in stand-replacement fire severity. If this is the case, the conditions on Smith Butte may offer some structural guidelines for managing fire severity in the eastern Washington physiographic province.

Although we have empirical data for changes between measurement periods, we relied on models for our fire behavior assessments. While BEHAVE appears relatively robust due to an extended history of use, the FFE extension to FVS is new and has several key assumptions related to important fire behavior variables. Height to live crown is a critical variable in the prediction of torching potential. It is defined in FFE as that height in the crown where canopy bulk density reaches 0.011 kg $m^{-3}$ in a 3 m horizontal slice through the crown (Scott and Reinhardt 2001). There are little data to validate this assumption. Canopy bulk density is expressed as the highest 5 m running mean of layers 0.3 m thick through the crown, yet another possible way to express it would be as the average through the crown from the base of live crown to the tree tops. Both of these would be subjective, but the latter would result in a decreased predicted crown fire behavior. Selection of an appropriate metric for height to live crown and canopy bulk density is a difficult challenge in the heterogeneous stand structures commonly found in forests in the eastern Cascade Mountains. The last model we used was FOFEM, which predicts mortality from a given flame length or scorch height based on bark thickness and crown dimensions. It is density independent and does not consider secondary mortality due to bark beetles or other agents, so it underpredicts mortality that may occur from synergistic disturbances. These are the strongest models we currently have, but their outputs should be used cautiously.

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## Literature Cited


Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D. C.

Agee, J. K. 1996. The influence of forest structure on fire behavior. Pages 52-68 Proceedings, 17th Annual Forest Vegetation Management Conference, Redding California.

Agee, J. K., B. Bahro, M. A. Finney, P. N. Omi, D. B. Sapsis, C. N. Skinner, J. W. van Wagtendonk, and C. P. Weatherspoon. 2000. The use of shaded fuelbreaks in landscape fire management. Forest Ecology and Management 127:55-66.

Albini, F. A. 1976. Estimating wildfire behavior and effects. USDA Forest Service General Technical Report INT-30. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Anderson, L., C.E. Carlson, and R. H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. Forest Ecology and Management 22:251-260.

Arno, S. F., D. G. Simmerman, and R. E. Keane. 1985. Forest succession on four habitat types in western Montana. USDA Forest Service General Technical Report INT-177. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Bell, J. F., and J. R. Dilworth. 1988. Log Scaling and Timber Cruising. Oregon State University Book Stores, Inc., Corvallis, Oregon.

Beukema, S., E. Reinhardt, J. Greenough, W. Kurz, N. Crookston, and D. Robinson. 2000. Fire and Fuels Extension: Model Description. Unpublished report by ESSA Technologies Ltd., Vancouver, B.C. for USDA Forest Service, Rocky Mountain Research Station, Moscow, Idaho. Available online at http://forest.moscowfsl.wsu.edu/gems/UsersGuideJuly2002.pdf.

Bradshaw, L., and E. McCormick. 2000. FireFamily Plus user's guide. USDA Forest Service General Technical Report RMRS-GTR-67-WWW. Rocky Mountain Research Station, Ogden, Utah.

Bright, G. 1941. Acreage by timber type in T7N, R11E. Unpublished map on file at Mt. Adams Ranger District Office, Gifford Pinchot National Forest, Trout Lake, Washington.

Brookes, M. H., J. J. Colbert, R. G. Mitchell, and R. W. Stark (Technical Coordinators). 1985. Managing tree and stands susceptible to western spruce budworm. USDA Forest Service Cooperative State Research Service. Technical Bulletin 1695. U.S. Government Printing Office, Washington D. C.

Brookes, M. H., R. W. Campbell, J. J. Colbert, R. G. Mitchell, and R. W. Stark (Technical Coordinators). 1987. Western Spruce Budworm. USDA Forest Service Cooperative State Research Service. Technical Bulletin 1694. U.S. Government Printing Office, Washington D. C.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Buchanan, J. B., L. L. Irwin, and E. L. McCutcheon. 1995. Within-stand nest site selection by spotted owls in the eastern Washington Cascades. Journal of Wildlife Management 59:301-310.

Burgan, R. E., and R. C. Rothermel. 1984. Fire behavior prediction and fuel modeling system – FUEL subsystem. USDA Forest Service General Technical Report INT-GTR-167. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Camp, A. E., C. Oliver, P. F. Hessburg, and R. Everett. 1997. Predicting late successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management 95:63-67.

Camp, A. E. 1999. Age structure and species composition changes resulting from altered disturbance regimes on the eastern slopes of the Cascades range, Washington. Journal of Sustainable Forestry 9:39-67.

Covington, W. W., R. L. Everett, R. Steele, L. L. Irwin, T. A. Daer, and. A. N. D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. Journal of Sustainable Forestry 2:13-63.

Dana, S. T., and S. K. Fairfax. 1980. Forest and Range Policy: Its Development in the United States. McGraw-Hill, New York.

Edmonds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, New York.

Everett, R., S. Martion, M. Bickford, R. Schellhaas, and E. Forsman. 1992. Variability and dynamics of spotted owl nesting habitat in eastern Washington. Pages 35-39 *In* D. Murphy (editor), Getting to the future through silviculture: workshop proceedings. USDA Forest Service General Technical Report INT-GTR-291. Intermountain Research Station, Ogden, Utah.

Filip, G. M. 1980. Disease Survey of Smith Butte in the Plough Sale Area, Mt. Adams Ranger District, Gifford Pinchot National Forest, Washington. Unpublished report on file at Forest Pest Management, State and Private Forestry, USDA Forest Service Region 6, Portland, Oregon.

Forest Ecosystem Management Assessment Team [FEMAT]. 1993. Forest ecosystem management: an ecological, economic, and social assessment. Portland, OR: U.S. Department of Agriculture; U.S. Department of the Interior [and others]. [Irregular pagination].

Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Franklin, J. F., F. C. Hall, C. T. Dyrness, and C. Maser. 1972. Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators. USDA Forest Service Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Ganey, J. L., and W. M. Block. 1994. A comparison of two techniques for measuring canopy closure. Western Journal of Applied Forestry 9:21-23.

Gifford Pinchot National Forest Soil Resource Inventory. 1971. Unpublished report on file at the Gifford Pinchot National Forest Headquarters, Vancouver, Washington.

Hadley, K. S., and T. T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. Canadian Journal of Forest Research 23:479-491.

Hessburg, P. F., R. G. Mitchell, and G. M. Filip. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. USDA Forest Service General Technical Report PNW-GTR-327. Pacific Northwest Research Station, Portland, Oregon.

Hummel, S., R. J. Barbour, P. F. Hessburg, and J. F. Lehmkuhl. 2001. Ecological and financial assessment of late-successional reserve management. USDA Forest Service Research Note PNW-RN-531. Pacific Northwest Research Station, Portland, Oregon.

King, G. M., K. R. Bevis, E. E. Hanson, and J. R. Vitello. 1997. Northern spotted owl management: mixing landscape and site-based approaches. Journal of Forestry 95:21-25.

McComb, W. and D. Lindenmayer. 1999. Dying, dead, and down trees. Pages 335-372 *In* M. Hunter editor, Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.

Mendez-Treneman, R. 2001. Biological Evaluation, Gotchen Fuels Project. Unpublished report on file in the Mt. Adams Ranger District Office, Gifford Pinchot National Forest, Trout Lake, Washington.

Mutch, R. W., S. F. Arno, J. K. Brown, C. E. Carlson, R. D. Ottmar, and J. L. Peterson. 1993. Forest health in the Blue Mountains: A management strategy for fire-adapted ecosystems. USDA Forest Service General Technical Report PNW-GTR-310. Pacific Northwest Research Station, Portland, Oregon.

Potter, A., J. Fleckenstein, S. Richardson, and D. Hays. 1999. Washington State unpublished status report for the Mardon Skipper. Washington Department of Fish and Wildlife, Olympia, Washington.

Prance, G. T., and A. E. Prance. 1993. Bark: The Formation, Characteristics, and Uses of Bark Around the World. Timber Press, Portland, Oregon.

Reinhardt, E. D., R. E. Keane, and J.K. Brown. 1997. First order fire effects model: FOFEM 4.0, user's guide. USDA Forest Service General Technical Report INT-GTR-344. Intermountain Research Station, Ogden, Utah.

Rothermel, R. C. 1983. How to predict the spread and intensity of forest and range fires. USDA Forest Service General Technical Report INT-143. Intermountain Research Station, Ogden, Utah.

Rothermel, R. C. 1991. Predicting behavior and size of crown fires in the northern Rocky Mountains. USDA Forest Service Research Paper INT-438. Intermountain Research Station, Ogden, Utah.

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Scott, J. H., and E. D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service Research Paper RMRS-RP-29. Rocky Mountain Research Station, Ogden, Utah.

Smith, D. M. 1962. The Practice of Silviculture. Wiley, New York.

Spies, T. A. 1998. Forest structure: a key to the ecosystem. Northwest Science 72:34-39.

Swetnam, T. W, and A. M. Lynch. 1993. Multi-century, regional-scale patterns of western spruce budworm outbreaks. Ecological Monographs 63:399-424.

Swetnam, T. W., B. E. Wickman, H. G. Paul, and C. H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since 1700 A.D. Research Paper PNW-RP-484. Pacific Northwest Research Station, Portland, Oregon.

Terry, R. D., G. V. Chilinger, and G. Varos. 1955. Summary of "Concerning some additional aids in studying sedimentary formations," by M. S. Shvetsov. Journal of Sedimentary Petrology 25:229-234.

Thomas, J. W., E. D Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the northern spotted owl. USDA, Forest Service; USDI, Bureau of Land Management; Fish and Wildlife Service; National Park Service. U.S. Government Printing Office, Washington, D. C.

Topik, C. 1989. Plant Association Guide and Management Guide for the Grand Fir Zone: Gifford Pinchot National Forest. USDA Forest Service Report R6-ECOL-TP-006-88. Pacific Northwest Region, Portland, Oregon.

United States Department of Agriculture. Forest Service. 1997. Late-successional reserve assessment. Pacific Northwest Region. Gifford Pinchot National Forest. Available online at http:// www.fs.fed.us/gpnf/mgtdir.

United States Department of Agriculture, Forest Service; USDI, Bureau of Land Management. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. U.S. Government Printing Office, Washington, D. C.

Van Wagner, C. E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23-34.

Willhite. E. A. 1999. Biological evaluation: western spruce budworm analysis units, Mount Adams Ranger District, Gifford Pinchot National Forest. WSCFID 99-1, Forest Insect and Disease Westside Service Center, Sandy Oregon. Available online at http:// www.fs.fed.us/r6/nr/fid/pubsweb/budworm.htm.

Williamson, N. M. 1999. Crown fuel characteristics, stand structure, and fire hazard in riparian forest of the Blue Mountains, Oregon. M.S. thesis, University of Washington, Seattle, Washington.

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# Isozyme Variation in Showy Stickseed, a Washington Endemic Plant, and Relatives

## Abstract

*Hackelia venusta,* a rare plant endemic to Chelan County, Washington, consists of two entities that differ most notably by flower color and geographic location. We evaluated the hypothesis that these entities are separate species using a phenotypic analysis of isozyme variation to compare both forms of *H. venusta* with sympatric and allopatric populations of the closely related *H. diffusa* var. *arida,* and with the allopatric taxa *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa*. Enzyme band phenotypes revealed that all populations were variable, with 60% to 80% polymorphic enzyme systems. Most variation was within population, with only 32% among population variation detected. The level of variation was moderate to high in *H. venusta* populations compared to other *Hackelia* populations. Enzyme band pattern data support the separation of *H. venusta* from *H. diffusa*. However, data do not provide evidence for the taxonomic separation of the two color forms of *H. venusta* at the species level. Regardless of the taxonomic recognition of *H. venusta* color forms, they should be conserved as rare extremes of *Hackelia* morphology and habitat preference.

## Introduction

*Hackelia venusta* (showy stickseed), of the family Boraginaceae, is a 2–4 dm, insect-pollinated, perennial plant endemic to steep rocky slopes covered with granite scree in Chelan County, Washington. The species was first described from a population in Tumwater Canyon at 488 m elevation (Piper 1924). The Tumwater Canyon population has white flowers with corolla limbs averaging 7.4 mm long, and is the only extant *H. venusta* population that has white flowers. Three additional Chelan County populations of 2–3 dm plants with smaller blue flowers (corolla limbs averaging 4.2 mm long) have been included in the *H. venusta* species concept (Carr 1974, Gentry and Carr 1976). These blue-flowered populations are located 16 km south southwest of the white-flowered population at ca. 2000 m elevation. The morphological and habitat differences between white-flowered and blue-flowered *H. venusta* support the hypothesis that the white- and blue-flowered populations represent two taxa (Gamon 1988). The taxonomic controversy is of particular current interest because *H. venusta* is considered endangered in Washington (Gamon 1988, Washington Natural Heritage Program 1991) and has been proposed for endangered species status (U.S. Fish and Wildlife Service 2000). The blue-flowered taxon is being described in another paper, but has no published name at this time. Therefore, in this paper we consistently refer to these plants as white- and blue-flowered forms of *H. venusta*.

The taxonomic status of *H. venusta* is complicated by morphological variation in the widespread taxon *H. diffusa* var. *arida* (sagebrush diffuse stickseed). *Hackelia diffusa* var. *arida* is a 4–6 dm species, and usually has small, white flowers that may be lightly washed with blue. However, three *H. diffusa* var. *arida* populations growing 5–40 km from the white-flowered *H. venusta* population are similar to white-flowered *H. venusta* in flower and fruit characteristics. Carr (1974) and Gentry and Carr (1976) suggested that the observed morphological similarities resulted from introgression from white-flowered *H. venusta* into nearby *H. diffusa* var. *arida*. *Hackelia diffusa* var. *arida* also intergrades with cream-colored *H.*

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*diffusa* var. *cottonii* (Columbia stickseed) in the Yakima area of Washington. In turn, *H. diffusa* var. *cottonii* intergrades with blue-flowered *H. diffusa* var. *diffusa* (western diffuse stickseed) in the Columbia Gorge (Gentry and Carr 1976). A recent analysis of *Hackelia* morphology supports recognizing *H. diffusa* var. *arida,* and the white- and blue-flowered components of *H. venusta* as separate but closely related taxa (Harrod et al. 1999).

Starch-gel electrophoresis was used to determine whether genetic data support recognition of white- and blue-flowered color forms of *H. venusta* as distinct species. Enzyme electrophoresis has been successfully employed in systematic studies of plants, largely because of its ability to quantify genetic similarities (Crawford 1989, Crawford 1990, Briggs and Walters 1997). To establish standards for evaluating taxonomic significance of electrophoretic variation in *H. venusta,* we sampled seven populations of *H. diffusa* var. *arida*, and one population each of *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa.* We scored enzyme variation in terms of phenotypic band similarity, and used these data to assess the magnitude of genetic variation within populations and the degree of similarity among populations. Variation and similarity within *H. diffusa* served as a template for judging *H. venusta* taxonomic rank. Under a phenetic species concept, species are distinct and distinguishable based on similarity (Winston 1999). Using a biological species concept, a species is defined as a reproductively isolated system of breeding populations (Winston 1999). Therefore, besides being characterized by lower genetic similarities (as in the phenetic species concept), congeneric species usually have fixed or consistent differences in isozyme alleles at some loci (biological species concept) (Avise 1994). If the *H. venusta* color forms are simply divergent populations of *H. diffusa* var. *arida,* we expect one or both forms will be more similar to the *H. diffusa* var. *arida* populations included in the study (all collected within 80 km of the *H. venusta* populations) than they are to *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa.*

Incidental to the taxonomic goal of this study, we addressed the concern that white-flowered *H. venusta* may have extremely limited variation compared to the blue-flowered form, as well as to *H. diffusa* populations. Genetic analysis of isozyme variation reveal that endemic plants often have limited variation (Hamrick and Godt 1990). However, measures of isozyme variation in populations of rare plants have been shown to be correlated with those measures in populations of their widespread congeneric relatives, and sometimes the endemic plants are more variable (Gitzendanner and Soltis 2000).

## Methods

Populations sampled included the one extant population of white-flowered *H. venusta,* one of the two extant populations of blue-flowered *H. venusta,* the same seven populations of *H. diffusa* var. *arida* examined in a morphological study (Harrod et al. 1999), and one population each of *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* (Table 1). The *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* populations were collected 190 and 320 km from

TABLE 1. *Hackelia* populations sampled in this study. *Hackelia venusta* (blue-flower) samples were micropropagated plantlets, and all other samples consisted of wild plant collections.

| Taxon | Acronym | Location | # individuals sampled |
|---|---|---|---|
| *H. venusta* (white-flower) | WFV | Tumwater Canyon, 9.6 km west of Leavenworth, WA | 22 |
| *H. venusta* (blue-flower) | BFV | Crystal Lake, 19.0 km southwest of Leavenworth, WA | 12 |
| *H. diffusa* var. *arida* | BM | Burch Mountain, 4.8 km northwest of Wenatchee, WA | 25 |
| *H. diffusa* var. *arida* | DC | Douglas Creek, 26.0 km north of Quincy, WA | 25 |
| *H. diffusa* var. *arida* | DE | Derby Canyon, 11.3 km southeast of Leavenworth, WA | 25 |
| *H. diffusa* var. *arida* | MC | Moses Coulee, 24.0 km north of Quincy, WA | 25 |
| *H. diffusa* var. *arida* | PE | Ponderosa Estates, 17.7 km north of Leavenworth, WA | 25 |
| *H. diffusa* var. *arida* | SC | Swakane Canyon, 19.3 km northeast of Wenatchee, WA | 25 |
| *H. diffusa* var. *arida* | TW | Tumwater Canyon, 1.6 km west of Leavenworth, WA | 25 |
| *H. diffusa* var. *cottonii* | COT | Rattlesnake Hills, near Moxee, WA | 29 |
| *H. diffusa* var. *diffusa* | DIF | Oneota Gorge near Multnomah Falls, OR | 30 |

the white-flowered *H. venusta* population. Due to the rarity of blue-flowered *H. venusta*, small samples of plant tissue were taken from the living plants and micropropagated (Edson et al. 1996). Only 12 plants were sampled, due to site inaccessibility and a desire to minimize negative impacts to the small populations. For the other populations, three to five leaves per plant were collected in the field and transported to the laboratory on ice. Voucher specimens of the *H. venusta* populations were deposited at the University of Washington herbarium. Vouchers for the *H. diffusa* populations were deposited at the herbarium of the Leavenworth Ranger District of the Okanogan and Wenatchee National Forests.

### Sample Preparation

Samples were prepared using NFGEL standard operating procedures (USDA Forest Service 1995). For each individual, 10 $mm^2$ of leaf tissue was ground in liquid nitrogen and proteins were extracted in a Tris buffer pH 7.5 (Gottlieb 1981). The resulting slurry was transferred to microtiter plate wells and stored at -70°C. For electrophoresis, the slurry was thawed and absorbed onto 3 mm wide wicks prepared from Whatman 3MM chromatography paper.

### Electrophoresis

Methods of electrophoresis follow the general methodology of Conkle et al. (1982) except that most enzyme stains are somewhat modified as outlined in USDA Forest Service (1995). A lithium borate electrode buffer (pH 8.3) was used with a Tris citrate gel buffer, pH 8.3 (Conkle et al. 1982), to resolve malic enzyme (ME), phosphoglucomutase (PGM), and phosphoglucose isomerase (PGI). A sodium borate electrode buffer (pH 8.0) was used with a Tris citrate gel buffer, pH 8.8 (Conkle et al. 1982), to resolve glycerate-2-dehydrogenase (GLYDH), glutamate-oxaloacetate transaminase (GOT), glucose-6-phosphate dehydrogenase (G6PDH), triosephosphate isomerase (TPI), and uridine diphosphoglucose pyrophosphorylase (UGPP). A morpholine citrate electrode and gel buffer, pH 8.0, was used to resolve isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), phosphogluconate dehydrogenase (6PGD), and shikimic acid dehydrogenase (SKD) (USDA Forest Service 1995). Two zones, designated F (faster) and S (slower), were resolved for each of the enzyme stains GOT, PGI, and UGPP, for a total of 15 enzyme systems. All enzymes were resolved on 11% starch gels. Enzyme stain recipes follow USDA Forest Service (1995) except that GOT was stained using the recipe from Wendel and Weeden (1989). Two people independently scored each gel. When they disagreed, a third person resolved the conflict. For quality control, 10% of the individuals were run and scored twice.

### Data Analysis

We performed a phenotypic analysis of isozyme variation. We use the term enzyme system here as a unit in a phenotypic analysis of isozymes. The enzyme system is a region of activity on an isozyme (starch) gel, which in a diploid plant would correspond to a single locus. In polyploids it corresponds to a set of loci that are homologous or homeologous (depending on the method of inheritance). All enzyme systems were scored for band patterns and band presence/absence. A band pattern consists of one to several bands. For a given enzyme system, all bands observed at a specific migration distance are treated as identical, even if they occur in different patterns. These data are suited for a phenotypic instead of genotypic analysis. Scoring starch gel electrophoresis data as enzyme band-pattern phenotypes has been successfully employed to describe how variation is partitioned within and among populations (Kahler et al. 1980, Poverene and Curvetto 1989, Vickery 1990, Chung et al. 1991, Dolan 1994, Rogers 1994, Samman et al. 2000, Wilson et al. 2000).

Phenotypic diversity measures were calculated from both band presence/absence and multi-banded patterns. For presence/absence data, phenotypic diversity was measured by a polymorphic index (PI), based on the frequency of occurrence of each band among individuals in a population (Chung et al. 1991). For multi-band patterns, phenotypic diversity measures include: (1) the number of band patterns found in each sampled population, (2) percent of enzyme systems that yield more than one band pattern, (3) the average number of band patterns per enzyme system in each population, and (4) Shannon-Weaver Diversity Index values (Shannon and Weaver 1949). The frequency of each enzyme band pattern was used to calculate the Shannon-Weaver Diversity Index. Larger Shannon-Weaver indices indicate more diverse populations. The distribution of the total variation within

and among populations was determined by partitioning the total Shannon-Weaver Diversity Index (Chung et al. 1991). The phenotypic relationships among populations were determined by calculating Hedrick's identities (Hedrick 1971) for multi-band pattern data, and cluster (UPGMA) analysis (Chung et al. 1991). Band pattern frequencies and the Shannon-Weaver Diversity Index were calculated using Popgene (Yeh et al. 1997), using the haploid codominant marker settings.

## Results

The *Hackelia* populations sampled were all variable, with 60-80% of the enzyme systems polymorphic, 38 – 50 bands present, and 2.00 – 3.40 multibanded patterns per enzyme system (Table 2). At the population level, isozyme variation in white-flowered *H. venusta* was moderate to high compared to other *Hackelia* populations. The blue-flowered *H. venusta* population was moderately variable. At the species level, *H. diffusa* var. *arida* was more variable than *H. venusta* at three diversity indicators (# bands, # patterns per enzyme system, and Shannon-Weaver diversity index). The isolated populations of *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* had the lowest levels of enzyme variability at all diversity measures. Over the entire study, most variation was within populations, with only 32% of the variation among populations. Of the total variation measured within each species, 20.3% of the variation was among populations in *H. diffusa* var. *arida*, and 14.2% was shared between the blue- and white-flowered populations of *H. venusta* (Table 2).

Most band patterns were shared among populations, but some were restricted to single taxa. Of the 100 enzyme patterns observed, 86 occurred in *H. diffusa* var. *arida,* and 78 (91%) of the patterns that occurred in *H. diffusa* var. *arida* also occurred in at least one other taxon. The remaining 14 of the 100 total band patterns occurred only in taxa other than *H. diffusa* var. *arida*. However, the individual bands making up eight of these patterns did occur in *H. diffusa* var. *arida.* The other six of the 14 patterns included a total of six bands not observed in *H. diffusa* var. *arida.* One of these six unusual patterns, occurring only in white-flowered *H. venusta,* lacked a TPI-F band observed in all other samples.

TABLE 2. Variation in *Hackelia* populations, revealed by starch-gel electrophoresis. N = mean sample size/enzyme system. %P = percent polymorphic enzyme systems. P.I. = polymorphic index. S.W. = Shannon-Weaver diversity index.

| Taxon: population | N | # bands | # unique bands | % P | # patterns/enzyme system (s.e.) | P.I. | S.W. | % S.W. among populations |
|---|---|---|---|---|---|---|---|---|
| *H. venusta* | 30.9 | 54 | 4 | 86.7 | 3.80 (0.51) | 0.380 | 0.747 | 14.2 |
| white | 19.1 | 50 | 4 | 80.0 | 3.40 (0.58) | 0.364 | 0.697 | |
| blue | 11.7 | 47 | 0 | 66.7 | 2.33 (0.41) | 0.337 | 0.577 | |
| mean | 15.4 | 48.5 | 2 | 73.4 | 2.87 | 0.351 | 0.637 | |
| H. diffusa var. *arida* | 134.5 | 65 | 12 | 80.0 | 5.73 (0.38) | 0.377 | 0.843 | 20.3 |
| BM | 22.9 | 44 | 1 | 73.3 | 3.07 (0.41) | 0.268 | 0.626 | |
| DC | 21.6 | 44 | 0 | 73.3 | 3.13 (0.47) | 0.308 | 0.652 | |
| DE | 16.3 | 48 | 3 | 66.7 | 3.00 (0.60) | 0.307 | 0.585 | |
| MC | 22.4 | 43 | 0 | 60.0 | 2.87 (0.48) | 0.231 | 0.537 | |
| PE | 15.1 | 50 | 0 | 80.0 | 3.13 (0.55) | 0.371 | 0.752 | |
| SC | 19.3 | 46 | 0 | 80.0 | 3.20 (0.48) | 0.349 | 0.752 | |
| TW | 18.0 | 38 | 0 | 60.0 | 2.64 (0.54) | 0.227 | 0.487 | |
| mean | 19.4 | 44.7 | 0.6 | 70.5 | 3.06 | 0.294 | 0.627 | |
| H. diffusa var. *cottonii* | 21.4 | 39 | 1 | 60.0 | 2.43 (0.38) | 0.237 | 0.460 | – |
| H. diffusa var. *diffusa* | 19.9 | 38 | 0 | 66.7 | 2.00 (0.24) | 0.217 | 0.410 | – |
| Total | 205.3 | 73 | – | 93.3 | 6.67 (0.38) | 0.414 | 0.926 | 31.8 |

We observed 73 bands in the 100 enzyme patterns, and 65 (89%) of these occurred in *H. diffusa* var. *arida*. One PGI-S band was unique to *H. diffusa* var. *cottonii*. One PGM band was unique to the *H. diffusa* var. *cottonii/H. diffusa* var. *diffusa* pair and occurred in all sampled individuals in those taxa. The white-flowered *H. venusta* population had four unique bands plus the unique absence of one band, however, all patterns unique to this population occurred at < 11% frequency. In contrast, only two of the seven sampled populations of *H. diffusa* var. *arida* had unique bands (one in BM and three in one pattern in DE). All the bands observed in blue-flowered *H. venusta* also occurred in *H. diffusa* var. *arida*, but not necessarily in the same combinations; three patterns (in PGI-S, TPI, and UGPP-F) occurred in blue-flowered *H. venusta* and not in *H. diffusa* var. *arida*.

Eight enzyme band patterns were shared only by *H. venusta* and those sampled *H. diffusa* var. *arida* populations (PE, SC, and TW) which had been hypothesized to show signs of introgression (Carr 1974). Three of these patterns (two in PGI-S and one in UGPP-S) occurred in moderate frequency (0.2 – 0.5) in white-flowered *H. venusta* and were rare or uncommon (frequency 0.05 – 0.11) in the *H. diffusa* var. *arida* populations in which they occurred.

Hedrick's similarities among populations of *H. diffusa* var. *arida* averaged 0.786 (range 0.667 to 0.934). Hedrick's similarities between *H. diffusa* var. *arida* and the other varieties of *H. diffusa* averaged less. Similarities to *H. diffusa* var. *cottonii* averaged 0.694 and those to *H. diffusa* var. *diffusa* averaged 0.706; none of the pairwise similarities exceeded 0.733. Hedrick's similarities between *H. diffusa* var. *arida* populations and *H. venusta* were lower yet, averaging 0.660 (range 0.561 – 0. 746) for white-flowered *H. venusta* and 0.634 (range 0.520 – 0.764) for blue-flowered *H. venusta*. Hedrick's similarities between *H. venusta* and the *H. diffusa* var. *arida* populations hypothesized to show introgression with *H. venusta* (Gentry and Carr 1976) were not statistically different from the similarities between *H. venusta* and other *H. diffusa* var. *arida* populations. These three *H. diffusa* var. *arida* populations appear no more similar to *H. venusta* than do the remaining four *H. diffusa* var. *arida* populations. Hedrick's similarity between the *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* populations sampled was 0.662. The similarity between white-flowered *H. venusta* and the blue-flowered *H. venusta* population sampled was 0.877 (Figure 1).

## Discussion

### Interpretation of Enzyme Band Patterns

Normally, an initial step in analyzing isozyme bands is to infer the alleles that produce the bands and thus determine genotypes of the individuals studied. We were unable to infer alleles from the *Hackelia* isozyme patterns for several reasons, including complicated band patterns, overlapping loci, and difficulty germinating seeds for crossing studies (Harrod 1999). Both *H. diffusa* and *H. venusta* are tetraploid (2n = 48) (Carr 1974). We are unaware of published information about the origin of that polyploidy (allopolyploid or autopolyploid) or the mode of inheritance of alleles (disomic or tetrasomic), and the evidence from isozyme phenotypes was inconsistent. In enzyme systems for which genetic interpretations could be provided (Weeden and Wendel 1989), genotypes fell into two categories. The combination of two different homozygous states (one-banded patterns) and at least one heterozygous state (suggestive of tetrasomic inheritance and autopolyploidy) was observed in GOT-F (2 populations), GOT-S (5 populations), SKD (5 populations of *H. diffusa*), and UGPP-F (3 populations). Fixed or excessive heterozygosity (suggestive of disomic inheritance and allopolyploidy) was observed for 6PGD and TPI-F in all populations and for SKD and UGPP-F in white-flowered *H. venusta*.

Genotypic interpretations were not readily inferred from dimeric PGI-S and TPI-F, which had complicated patterns often involving five to seven bands, and monomeric UGPP-F, which often had three or more bands. Additionally, presumed loci overlapped in PGM (2 – 4 bands in a restricted area of the gel) and MDH (one band in 90% of individuals). In theory, genetics of *Hackelia* isozymes might have been clarified by examining progeny arrays of wild plants or by examining isozymes in seedlings produced by controlled crosses. However, seed set is low in wild plants and no seed has been produced in controlled crosses (Harrod 1999).

### Enzyme Variation

Conserving biodiversity involves preserving within-taxon diversity. All the *Hackelia* populations

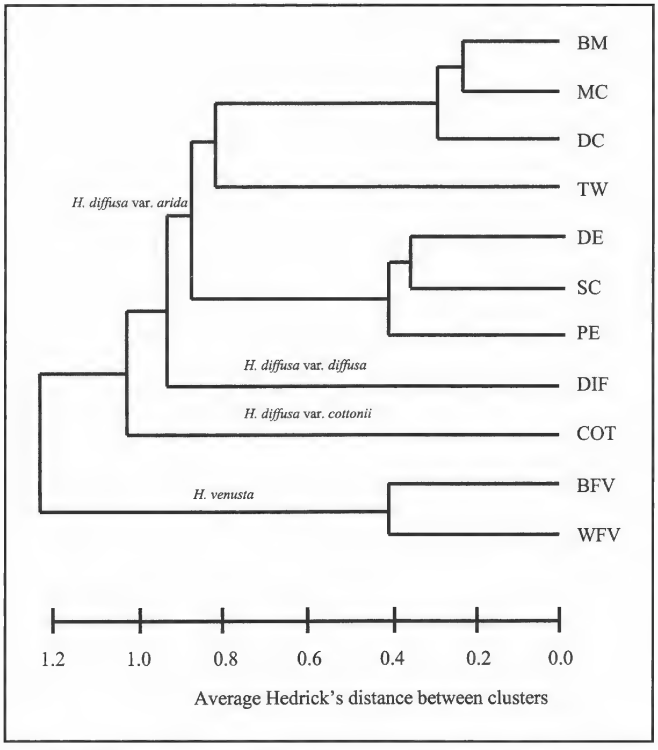


Figure 1. UPGMA dendrogram of *Hackelia* populations, based on Hedrick's distances among populations, which were calculated from band frequency data. WFV and BFV = white- and blue-flowered *H. venusta,* respectively. See Table 1 for acronyms.

studied were variable (Table 2). Although endemic plants often have limited isozyme variation (Hamrick and Godt 1990), white-flowered *H. venusta* and the nearby PE and SC populations of *H. diffusa* var. *arida* had the highest measures of variability. At the population level, all measures of variation were higher in white-flowered *H. venusta* than in the average population of *H. diffusa* var. *arida.* The high level of variation in white-flowered *H. venusta* is consistent with the observation that endemic plants are sometimes more variable than their widespread congeneric relatives (Gitzendanner and Soltis 2000). Phenotypic analysis of enzyme band patterns provides no reason to believe that lack of overall genetic variation limits survival of white-flowered *H. venusta.* The population may be specialized in some way, however, perhaps requiring high magnesium substrates (St. John 1929).

Blue-flowered *H. venusta* was also variable, but most measures of enzyme variation were lower than the average for *H. diffusa* var. *arida* populations (Table 2). This may be an artifact of sampling because only 12 micropropagated blue-flowered plantlets were available for this study.

### Taxonomic Rank of White- and Blue-flowered *Hackelia venusta*

In general, populations of different congeneric species are distinguished by low genetic identities (Nei 1978). Genetic identities among congeneric species average 0.68, while those between populations of the same species are usually > 0.9 (Crawford 1989). However, not all pairs of related species meet this expectation. Some pairs of congeneric species have genetic identities > 0.99 and as low as 0.25 (Crawford 1989). We use Hedrick's similarities (Hedrick 1971) as a phenetic

measure of population similarity to assess the taxonomic rank of *H. venusta* color forms using a phenetic species concept (Winston 1999).

Hedrick's similarities clearly separate *H. venusta* from *H. diffusa* (Figure 1). Similarities average highest among *H. diffusa* var. *arida* populations and lowest between populations of *H. venusta* and *H. diffusa* var. *arida*. Therefore, *H. venusta* populations cluster farther from *H. diffusa* var. *arida* than the taxonomically recognized *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* (Figure 1). These enzyme data support the morphological data that recognize *H. venusta* and *H. diffusa* as closely related taxa (Carr 1974, Gentry and Carr 1976, Harrod et al. 1999), despite the intermediate appearance of a few *H. diffusa* var. *arida* populations (Carr 1974, Gentry and Carr 1976). Blue- and white-flowered *H. venusta* are more similar (Hedrick's similarity = 0.877) than most pairs of *H. diffusa* var. *arida* populations. Also, the *H. venusta* color forms are less similar to *H. diffusa* var. *arida* than are the named varieties *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* (Figure 1). Enzyme phenotype data alone do not provide evidence for a taxonomic separation of the forms using a phenetic species concept (Winston 1999).

When comparing band presence/absence between *H. venusta* color forms, the white-flowered form had four unique bands and one unique absence of a band. However, all these unique bands occurred at low frequencies. In fact, no fixed band difference distinguished *H. diffusa* var. *cottonnii* from *H. diffusa* var *diffusa*, or *H. diffusa* var. *arida* from *H. venusta*, providing no evidence for taxonomic separation of the color forms using a biological species concept (Winston 1999). Although the enzyme phenotypic data do not support species level recognition of the *H. venusta* color forms, blue- and white-flowered *H. venusta* are readily and consistently differentiated from each other by flower color, flower size, and habitat (Harrod et al. 1999).

### Implications for Management

Preserving the large levels of diversity found among *Hackelia* populations will require preserving the genetic extremes represented by white- and blue-flowered *H. venusta*. It is necessary to preserve both color forms whether we label white- and blue-flowered *H. venusta* as conspecific populations, as distinct varieties, or as distinct species. To preserve genetic variation and prevent loss of the rarer alleles, large populations should be maintained in the wild. Off-site germplasm banks should include collections from as many different individuals as practical.

Although we hope this enzyme study contributes to the conservation of *Hackelia* biodiversity, immediate decisions crucial to *Hackelia* conservation must be based on entirely different criteria. If preserving white- and blue-flowered *H. venusta* is a priority, management should be driven by concerns about demographics. The only extant population of white-flowered *H. venusta* has severely declined in number over the last two decades. Since 1992, one population of blue-flowered *H. venusta* has been extirpated by a landslide and the two remaining populations are small. Questions of taxonomy and genetic diversity will be moot if these plants become extinct.

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## Literature Cited

Avise, J. C. 1994. Molecular Markers, Natural History and Evolution. Chapman and Hall, New York.

Briggs, D., and S. M. Walters. 1997. Plant Variation and Evolution. Cambridge University Press, United Kingdom.

Carr, R. L. 1974. A taxonomic study in genus *Hackelia* in western North America. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Chung, M. G., J. L. Hamrick, S. B. Jones, and G. S. Derda. 1991. Isozyme variation within and among populations of *Hosta* (Liliaceae) in Korea. Systematic Botany 16:667-684.

Conkle, M. T., P. D. Hodgskiss, L. B. Nunnally, and S. C. Hunter. 1982. Starch Gel Electrophoresis of Conifer Seeds: A Laboratory Manual. USDA Forest Service General Technical Report PSW-64. Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Crawford, D. J. 1989. Enzyme electrophoresis and plant systematics. Pages 146 – 164 *In* D. E. Soltis and P. S. Soltis (editors), Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

Crawford, D. J. 1990. Plant Molecular Systematics. Wiley, New York.

Dolan, R. W. 1994. Patterns of isozyme variation in relation to population size, isolation, and phytogeographic history in royal catchfly (*Silene regia;* Caryophyllaceae). American Journal of Botany 81:965-972.

Edson, J. L., A. D. Leege-Brusven, R. L. Everett, and D. L. Wenny. 1996. Minimizing growth regulators in shoot culture of an endangered plant, *Hackelia venusta* (Boraginaceae). In Vitro Cellular and Developmental Biology - Plant 32:267-271.

Gamon, J. 1988. Habitat management guidelines for *Hackelia venusta* on the Wenatchee National Forest. Washington Natural Heritage Program, Olympia, Washington.

Gentry, J. L., Jr., and R. L. Carr. 1976. A revision of the genus *Hackelia* (Boraginaceae) in North America, north of Mexico. Memoirs of the New York Botanic Gardens 26:121-227.

Gitzendanner, M. A., and P. S. Soltis. 2000. Patterns of genetic variation in rare and widespread plant congeners. American Journal of Botany 87:783-792.

Gottlieb, L. D. 1981. Gene number in species of Asteraceae that have different chromosome numbers. Proceddings of the National Academy of Sciences USA 78:3726-3729.

Hamrick, J. L., and M. J. W. Godt. 1990. Allozyme diversity in plant species. Pages 43-63 *In* A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (editors), Plant Population Genetics, Breeding, and Genetic Resources. Sinauer Associates, Inc., Sunderland, Maryland.

Harrod, R. J. 1999. Unsuccessful pollination experiments with *Hackelia venusta.* Douglasia, Occasional papers 7:51-52.

Harrod, R. J., A. Malmquist, and R. L. Carr. 1999. A review of the taxonomic status of *Hackelia venusta* (Boraginaceae). Rhodora 101:16-27.

Hedrick, P. W. 1971. A new approach to measuring genetic similarity. Evolution 25:276.

Kahler, A. L., R. W. Allard, M. Krzakowa, C. F. Wehrhahn, and E. Nevo. 1980. Associations between isozyme phenotypes and environment in the slender wild oat (*Avena barbata*) in Israel. Theoretical and Applied Genetics 56:31-47.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583-590.

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Piper, C. V. 1924. New flowering plants of the Pacific Coast. Proceedings of the Biological Society of Washington 37:91-96.

Poverene, M. M., and N. P. Curvetto. 1989. Esterase isozyme variation in the *Eragrostis curvula* complex (Poaceae). Plant Systematics and Evolution 166:173-181.

Rogers, D. L. 1994. Spatial patterns of allozyme variation and clonal structure in coast redwood (*Sequoia sempervirens*). Ph.D. Dissertation, University of California, Berkeley, California.

Samman, S., V. D. Hipkins, and B. L. Wilson. 2000. Genetic variation in ponderosa pine, bitterbrush, and Idaho fescue, community-dominant plants of California's yellow pine forest. Madroño 47:164-173.

Shannon, C. E., and W. Weaver. 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois.

St. John, H. 1929. New and noteworthy northwestern plants. Research Studies, State College of Washington 1:104 – 105.

USDA Forest Service. 1995. National Forest Genetic Electrophoresis Laboratory (NFGEL) Standard Operating Procedures. USDA Forest Service, Camino, California.

U.S. Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants: proposed endangered status for the plant *Hackelia venusta* (showy stickseed). Federal Register 65(30):739-7346.

Vickery, R. K., Jr. 1990. Close correspondence of allozyme groups to geographic races in the *Mimulus glabratus* complex (Scrophulariaceae). Systematic Botany 15:481-496.

Washington Natural Heritage Program. 1991. Endangered, threatened, and sensitive vascular plants of Washington. Department of Natural Resources, Olympia, Washington.

Weeden, N. F., and J. F. Wendel. 1989. Genetics of plant isozymes. Pages 46 – 72 *In* D. E. Soltis and P. S. Soltis (editors), Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

Wendel, J. F., and N. F. Weeden. 1989. Visualization and interpretation of plant isozymes. Pages 5 – 45 *In* D. E. Soltis and P. S. Soltis (editors), Isozymes in Plant Biology. Dioscorides Press, Portland, Oregon.

Wilson, B. L., D. L. Doede, and V. D. Hipkins. 2000. Isozyme variation in *Sisyrinchium sarmentosum* (Iridaceae). Northwest Science 74:346-354.

Winston, J. E. 1999. Describing Species. Columbia University Press, New York.

Yeh, F. C., R.-C. Yang, and T. Boyle. 1997. Popgene Version 1.20. University of Alberta, Edmonton, Alberta.

# Northwest Science Notes

*The purpose of Notes is to publish papers typically less than five pages long. No specific format or content is required for articles published as Notes, but all will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.*

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## A Small Drop-Net versus Clover Traps for Capturing Mule Deer in Southeastern British Columbia

### Abstract

Clover traps are commonly used for capturing wild deer, particularly when the absence of open flat terrain precludes other methods. Clover traps can be inefficient because of non-target captures, escapes, and a reluctance of deer to enter the trap. To increase capture efficiency, we devised a small inexpensive drop-net for capturing targeted mule deer in steep forested terrain. We suggest that drop-netting may be more efficient, primarily by eliminating non-target captures. We recommend considering the use of drop-nets anywhere Clover trapping is used or considered.

### Introduction

Several techniques have been developed for capturing wild deer. Among the more common techniques are Clover traps (Clover 1954, McCullough 1975, Haulton et al. 2001), box traps (Haulton et al. 2001), rocket nets (Hawkins et al. 1968), darting (Kilpatrick et al. 1997), drive-netting (Sullivan et al. 1991), and drop-netting (Ramsey 1968, Conner et al. 1987). Many of these techniques require high deer densities in flat open terrain. Clover traps are commonly used because they are portable, relatively inexpensive to build, and can be used in closed forest conditions. However, clover traps require animals to enter an enclosed trap, be entirely within the trap, and subsequently trip a baited door-release mechanism. Deer are often reluctant to enter the relatively enclosed space of the trap, trap malfunctions are common, and non-target species are often captured. These failed target-captures increase project expense by increasing the amount of time and resources spent capturing target deer. Clover traps have also been associated with high rates of capture mortality and myopathy (Haulton et al. 2001). To increase capture efficiency, we developed a small drop-net apparatus for capturing wild mule deer (*Odocoileus hemionus*) in the Selkirk Mountains of southeastern British Columbia. Our objectives were to provide details of this apparatus and offer comparisons and recommendations relative to Clover traps for capturing wild mule deer in mountainous, forested terrain.

### Study Area

The trap site was located in the Selkirk Mountains near the mouth of Lemon Creek, ~23 km northwest of Nelson, British Columbia. Terrain in the area was generally steep and broken with slope gradients commonly > 45° and elevations ranging from 548 m to 2,405 m. The surrounding

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landscape was dominated by coniferous forest interspersed with logging roads and harvest blocks. Trap and drop-net sites were located on a 1-km section of unplowed logging road on a steep (35°) forested slope within a traditional mule deer winter range area. Snow was persistent on the ground from December to March at trap sites. White-tailed deer (*Odocoileus virginianus*) are sympatric to mule deer in this area and were present during trapping.

## Methods

### Clover Traps

Trapping occurred between 22 January and 10 March in 1998–2002. Adult mule deer were our target individuals. We always preceded trapping efforts by pre-baiting alfalfa 5–7 days before setting traps, to attract deer to sites and provide a degree of habituation. During this pre-baiting phase, modified clover traps (McCullough 1975) were in place, but not set for capture. Clover traps can be constructed relatively inexpensively from locally available hardware and netting suppliers.

Following pre-baiting, we set one trap at each of three pre-baiting sites. We set traps in mornings and left them unattended until the following morning. Traps were baited and monitored by a single person. If a trap contained a captured deer, additional handlers were called to the site to assist with handling. Captured target deer were physically restrained by handlers, blindfolded, fitted with a radiocollar equipped with a mortality sensor, then released immediately after handling was complete. Non-target deer (white-tailed deer and fawns) were released immediately without handling. Radiocollared deer where relocated within 1–3 days following handling and thereafter 1-3 times per month for ~ 1 yr, and thus permitted us to monitor capture myopathy rates.

### Drop-Net

In January 2002, we constructed and used a small drop-net apparatus (Figure 1) in conjunction with our Clover trapping efforts. One person constructed the apparatus in 4 hr using basic tools and materials bought at a local hardware store, and a 6.1-m x 6.1-m piece of netting purchased from a netting supply outlet. Total cost of materials to construct the drop-net was similar to the cost of one clover trap.

We pre-baited the capture area in the fashion described for Clover trapping and chose a single site with suitable rigging trees 50 m from a Clover trap location. We positioned the drop-net over the center of a wide (10 m) section of unplowed logging road. We suspended the net 1 m and 2 m above compacted snow using ropes attached to trees on either side of the road (Figure 1). One person took ~2 hr to install the drop-net, which was in place during pre-baiting.

Following the pre-baiting period, a small amount of alfalfa was placed, as bait, on the snow directly beneath the center of the drop-net. We attached a 60-m cord to a release mechanism (Figure 1) and extended the cord to a location out of visual range. A concealed spotter signaled when target deer were beneath the drop-net. We then released the drop-net by pulling on the 60-m cord, which activated the release mechanism. Captured deer were handled similar to that described for clover traps.

## Results

During four annual trapping periods, we captured 26 deer in Clover traps: 15 target and 11 non-target (2 fawns, 9 white-tailed deer). All Clover trap captures were of single deer. At least three deer escaped from traps. Trapping effort per target deer with Clover traps was calculated as 18.3 hr in the first year, 27.8 hr in the second year, 46.3 hr in the third year, and 21.5 hr in the fourth year (based on time spent by one person monitoring traps and handling deer, plus additional handler time). Drop-netting was only used in the final year and we captured three mule deer by this means. Of three capture attempts with the drop-net, the first attempt resulted in a deer escaping before being engulfed by the drop-net. Upon resetting the net 1 m from the ground, the second attempt resulted in two captured target deer, which we chemically immobilized for handling. The third attempt resulted in one captured target deer, which we physically restrained for handling. Effort for drop-netting was calculated as 9.0 hr/target-deer. We did not observe any cases of capture mortality among any captured deer or any cases of capture myopathy among radiocollared deer.

## Discussion

In previously reported cases of drop-netting, high-density white-tailed deer were captured in flat open

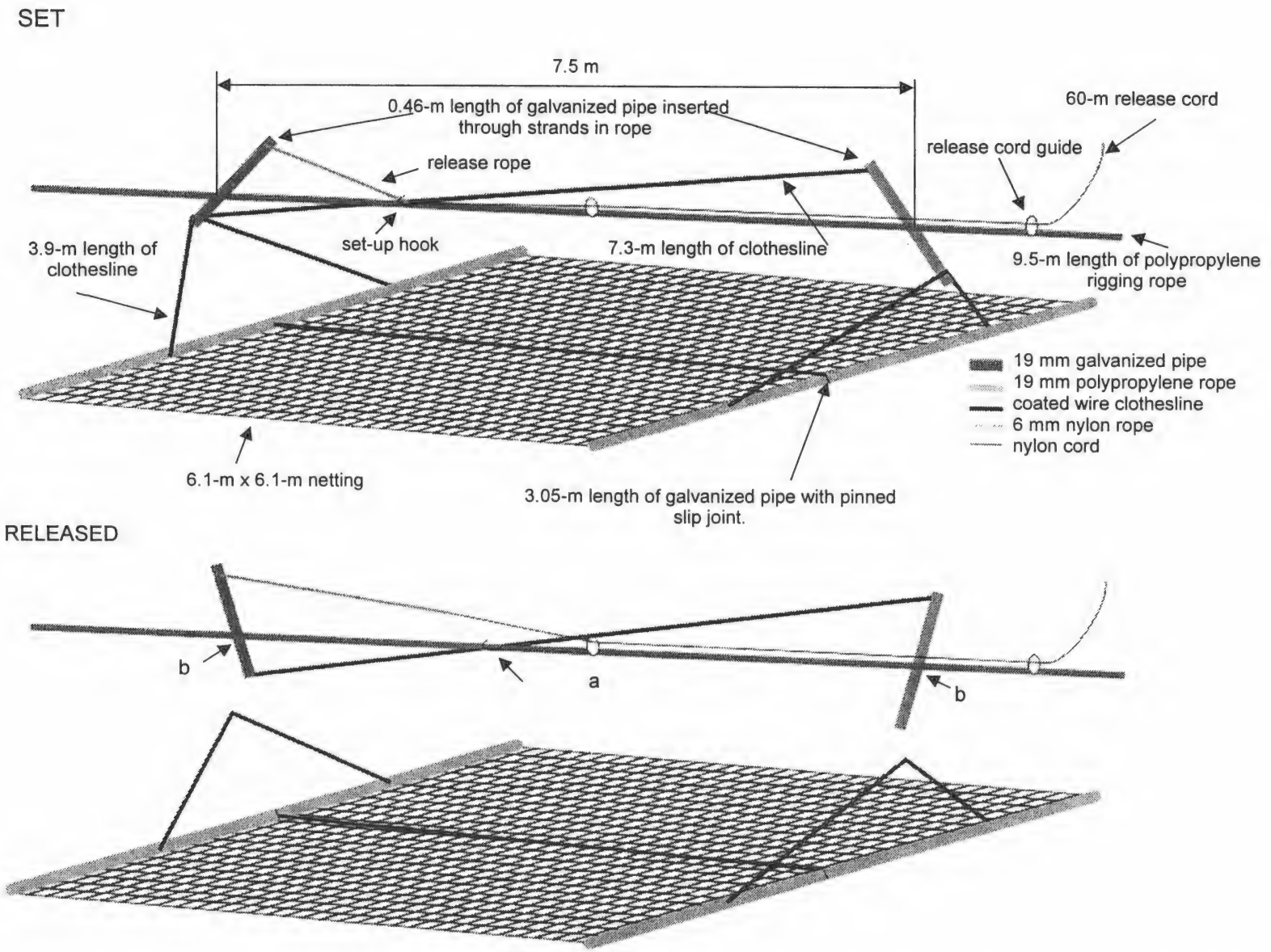


Figure 1. A small drop-net apparatus for capturing deer. The net was suspended 1.0 m from the ground between 2 large trees on either side of an unplowed logging road in steep forested terrain. A 60-m release cord was used to trigger the net. The release rope was hooked on the set-up hook to prevent release of the net during set-up. Pulling the release cord separated the release rope from the hook at a. Releasing the release cord forced the 2 pieces of 0.46-m galvanized pipe to pivot at b and allowed the net to fall.

conditions using a 17.8-$m^2$ net (Ramsey 1968) and 21.3-$m^2$ net (Conner et al. 1987). Such large nets with elaborate set-ups requiring flat open ground were not an option to us in this heavily forested and steep environment, somewhat typical of mule deer wintering habitat in the Pacific Northwest (Shackleton 1999). We found the 6.1 $m^2$ net was an optimal size for rigging between trees and suspension over an unplowed logging road, the only source of open flat ground.

While fewer deer can be captured simultaneously using a smaller net, multiple captures have resulted in high rates of capture mortality and myopathy (Conner et al. 1987). Beringer et al. (1996) found survival of rocket-netted deer was most influenced by the number of deer captured together and that deer captured in groups of two or more were at proportionately greater risk than those captured alone. Thus, we believe the control of a smaller net in facilitating the capture and selection of individual deer is beneficial. This was especially important because both white-tailed deer and mule deer were present. Indeed, almost half of our total captures using clover traps were non-target individuals resulting in wasted effort and resources.

If Clover traps are being considered or used to capture deer, a fundamental requirement is that deer must be attracted to bait in sufficient densities to make the effort worthwhile. If this is the case, we suggest that drop-netting may be a more efficient option. Regrettably, we cannot yet report extensive use of this small drop-net, and our effort calculations cannot reliably be compared. However, we believe in comparison to Clover trapping, drop-netting presents a potential increase in capture efficiency, primarily due to eliminating non-target captures and escapes, and a greater willingness of deer to walk underneath a drop-net compared to their willingness to enter a Clover trap. As well, the low cost and ease of use of this drop-net provides a low investment alternative. We recommend this small and relatively simple drop-net method be considered anywhere Clover trapping is used or considered.

## Acknowledgments

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## Literature Cited

Beringer, J., L. P. Hansen, W. Wilding, J. Fisher, and S. L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management 60:373-380.

Clover, M. R. 1954. A portable deer trap and catch-net. California Fish and Game 40:367-373.

Conner, M. C., E. Soutiere, and R. A. Lancia. 1987. Drop-netting deer: costs and incidence of capture myopathy. Wildlife Society Bulletin 15:434-438.

Hawkins, R. E., L. D. Martoglio, and G. G. Montgomery. 1968. Cannon-netting deer. Journal of Wildlife Management 32:191-195.

Haulton, S. M., W. F. Porter, and B. A. Rudolph. 2001. Evaluating 4 methods to capture white-tailed deer. Wildlife Society Bulletin 29:255-264.

Kilpatrick, H. J., S. M. Spohr, and A. J. DeNicola. 1997. Darting urban deer: techniques and technology. Wildlife Society Bulletin 25:542-546.

McCullough, D. R. 1975. Modification of the Clover deer trap. California Fish and Game 61:242-244.

Ramsey, C. W. 1968. A drop-net deer trap. Journal of Wildlife Management 32:187-190.

Shackleton, D. 1999. Hoofed Mammals of British Columbia. University of British Columbia Press, Vancouver, British Columbia, Canada.

Sullivan, J. B., C. A. DeYoung, S. L. Beasom, J. R. Heffelfinger, S. P. Coughlin, M. W. Hellickson. 1991. Drive-netting deer: incidence of mortality. Wildlife Society Bulletin 19:393-396.

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# NORTHWEST SCIENCE

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This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum may not be peer-reviewed so that publication is expedited. The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

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- Literature Cited
- Footnotes
- Tables
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Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

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Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

### *Online (web) references*

USDA Forest Service. 1998. Fire effects information system. Prescribed Fire and Fire Effects Research Work Unit, Rocky Mountain Research Station, Missoula, Montana. Available online at www.fs.fed.us/database/feis/

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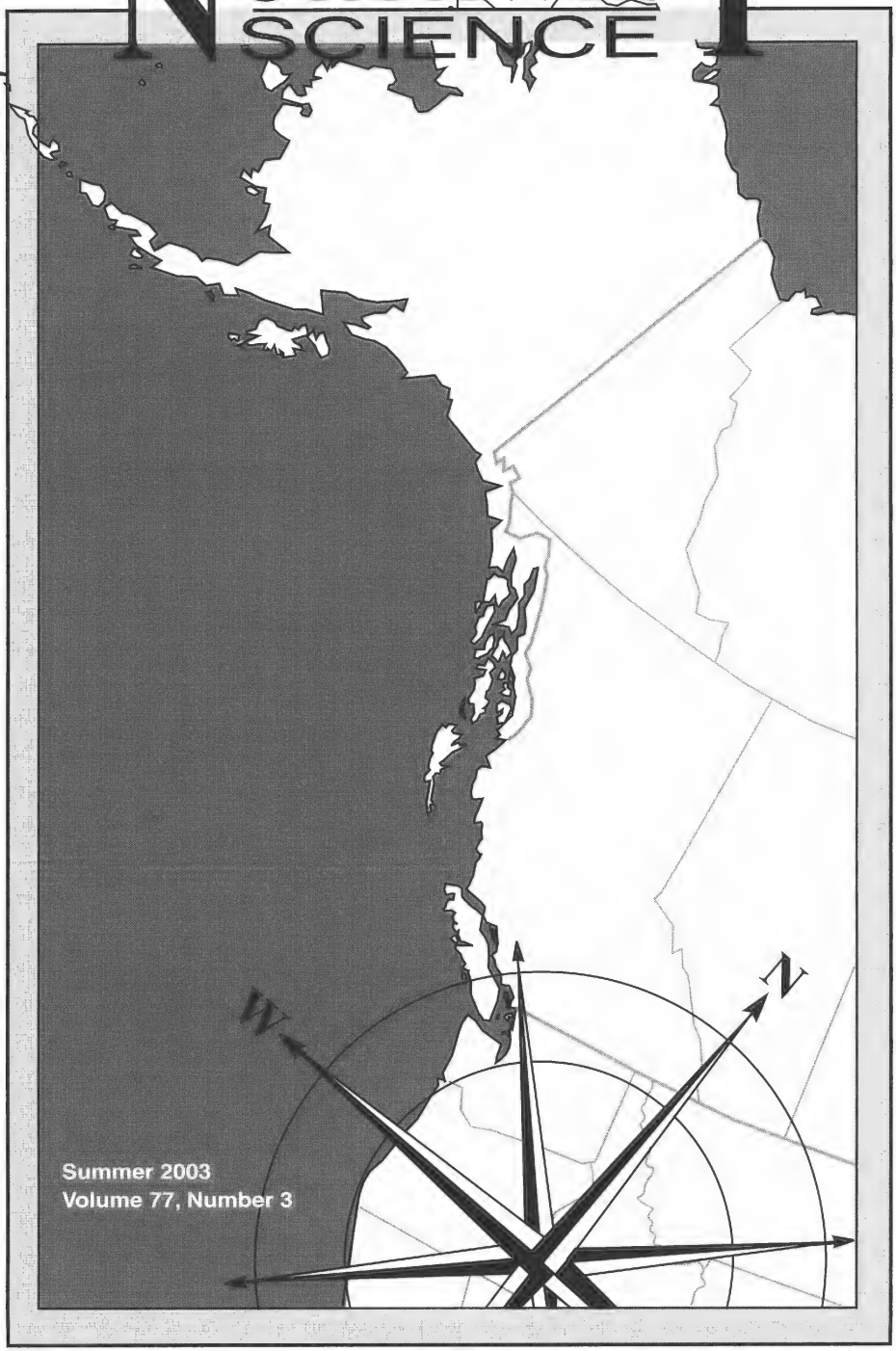


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# Announcements

## Annual Meeting, Central Washington University, March 24-27, 2004

The 77th annual meeting of the Northwest Scientific Association will be hosted by Central Washington University in Ellensburg, Washington from Wednesday 24 March to Saturday 27 March, 2004. Following a business meeting of the governing board on 24 March, scientific sessions will occur on the following two days with a variety of concurrent sessions and symposia including Natural Areas, Shrub-Steppe Ecosystems, and the Yakima River Basin. The Society for Northwestern Vertebrate Biology will also meet concurrently with the NWSA. Field trips will be offered to several sites in and around the Yakima River Basin on Saturday March 27.

Members and non-members are welcome at the annual meeting. Students are especially encouraged to attend and report the results of their research. Anyone interested in helping to organize or chair sessions should contact Karl Lillquist, Geography and Land Studies Department, Central Washington University, Ellensburg, WA 98926, telephone (509) 963-1184, fax (509) 963-1047 or email: lillquis@cwu.edu. A call for abstracts and meeting registration will be mailed to all members of the Northwest Scientific Association.

## Call for Nominations

Nominations are invited for Honorary Life Member and Outstanding Scientist awards for the year 2004. Honorary Life Memberships are awarded to individuals who have worked for the continuing success of the Northwest Science Association with selfless enthusiasm and devotion. Outstanding Scientists are individuals who have made significant contributions to our understanding of basic or applied scientific issues that are especially relevant to northwestern North America. Recognition of Honorary Life Members and Outstanding Scientists is an important activity of the Northwest Science Association. Nominations for both awards should be sent to Paul Verrell (E-mail: verrell@wsu.ed) as soon as possible, and certainly not later than 1 January 2004.

**Todd A. Sanders**[1] and **Robert L. Jarvis,** Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

# Band-tailed Pigeon Distribution and Habitat Component Availability in Western Oregon

## Abstract

Abundance of Pacific coast band-tailed pigeons has declined; this decline is thought to be due, in part, to habitat alteration associated with current forestry practices. We examined distribution of Pacific coast band-tailed pigeons and availability of habitat components (known mineral sites and potential nesting and feeding areas) in the central Coast Range of Oregon. Also, we evaluated associations of relative pigeon abundance at 323 randomly selected sample points and 97 known nest sites with adjacent habitat component availability. We detected 1–8 pigeons during a 1-hr point count at 83% of sample points from mid-June to July. Eighty-four percent of the study area was classified as potential nesting (66%) and feeding (18%) areas. The maximum distance to the closest known mineral site was 37 km, but 91% of the study area was within 25 km of the nearest known mineral site. Availability of habitat components around known nest sites was similar to that at sample points and reflected availability within the study area. Relative pigeon abundance was not associated with availability of known mineral sites, or potential nesting and feeding areas. Pigeons were 62% more abundant along the western one-third of the Coast Range than along the eastern one-third, however, and this pattern was correlated with the apparent availability of red elder and cascara. Possibly the availability of red elder and cascara imposed a constraint on band-tailed pigeon distribution and abundance.

## Introduction

The abundance of Pacific coast band-tailed pigeons (*Columba fasciata monilis*), which nest mostly in coastal areas of British Columbia, Washington, Oregon, and California, decreased by 2.8% annually between 1966 and 2000 and by 1.5% annually between 1991 and 2000 as indicated by the Breeding Bird Survey (analysis provided by J.R. Sauer, U.S. Geological Survey, Laurel, Maryland). This decline has been corroborated by visual counts conducted during August at mineral sites in Oregon and audio counts conducted during June in Washington (Western Migratory Upland Game Bird Technical Committee 1994). Increasingly restrictive hunting regulations have been implemented since the late 1980s, but population trends apparently have not been reversed (Western Migratory Upland Game Bird Technical Committee 1994). The decline is suspected to be related, in part, to extensive timber harvest and intensive reforestation replacing diverse forest stands with even-age conifer monocultures that reduce availability of food producing trees and shrubs (Hansen et al. 1991, Braun 1994, Western Migratory Upland Game Bird Technical Committee 1994).

Effective management of an animal population requires knowledge of its size and composition, and how the population relates to habitat and other limiting factors (Verner 1981, Wiens and Rotenberry 1981, Hansen et al. 1993). Little is known about the distribution of band-tailed pigeons and availability of habitat in the Pacific Northwest. Leonard (1998) radio-marked 127 adult band-tailed pigeons in the central Oregon Coast Range and measured breeding season home range size ($\bar{x}$ = 11,121 ha) and described 137 nest, feeding, and mineral sites. He suggested that pigeons select nest sites based on availability of mineral sites and potential nesting and feeding areas.

Band-tailed pigeons in Oregon nest primarily in Douglas-fir (*Pseudotsuga menziesii*) trees within closed-canopy (>70%), conifer or mixed conifer-broadleaf forests (Leonard 1998). Pigeons feed almost exclusively on berries of red elder (*Sambucus racemosa*), blue elder (*S. cerulea*), and cascara (*Rhamnus purshiana*) during the breeding season (Jarvis and Passmore 1992). Pigeons also congregate at and use mineral sites (March and Sadleir 1972, Jarvis and Passmore 1992, Sanders and Jarvis 2000). In Oregon, mineral sites are typically mineralized springs, abandoned artesian salt wells, and saltwater bays and estuaries, but also may be exposed mineral deposits and

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mineralized wastewater from pulp mills (Sanders and Jarvis 2000).

Food plays a major role in band-tailed pigeon ecology, influencing distribution (Neff 1947), initiation and duration of the nesting season (Gutiérrez et al. 1975, Jarvis and Passmore 1992), and use of mineral sites (Sanders and Jarvis 2000). In the Coast Range, elder and cascara shrubs are naturally prevalent in disturbed, open-canopy forests of early to intermediate successional stages and some riparian areas (Franklin and Dyrness 1988, Kozloff 1976, Klinka et al. 1989, Leonard 1998, Pabst and Spies 1998). Berries of red elder and cascara provide a dependable and nutrient-rich food supply during the nesting season (Sanders 1999). Red elder berries are consumed from late June to mid-August and cascara berries from late August to early September, consistent with the fruiting phenology of these shrubs (Jarvis and Passmore 1992). Berries of blue elder become available in early September and are consumed in September and October.

In western Washington, Oregon, and northern California, forests have been harvested extensively for >100 yr (Tappeiner et al. 1997). These are among the most productive coniferous forests in the world and forestry practices are intense (Franklin and Dyrness 1988, Harris 1984). Since the mid-1940s, silvicultural systems have typically included clear-cutting, broadcast burning of logging slash, hand planting of selected species, pre-commercial and commercial thinning, application of herbicides to suppress competing species, and harvesting at 40–100 yr intervals, although 40–60 yr intervals are more common (Hansen et al. 1991, Spies et al. 1991, Tappeiner et al. 1997). Intensive reforestation practices suppress the growth of red elder, blue elder, and cascara, primarily through application of herbicides and overstory shading (Hansen et al. 1991). Such forestry practices also produce a greatly altered forest environment, resulting in a mosaic of patches of forest stands across the landscape (Hansen et al. 1991). The spatial pattern of vegetation exerts strong influence on the abundance, distribution, and dynamics of populations inhabiting those landscapes (Harris 1984, Wiens 1989). The extent to which forestry practices impact band-tailed pigeon demographics is unknown, but the potential is substantial.

We examined the distribution of band-tailed pigeons and availability of habitat components (known mineral sites and potential nesting and feeding areas) to test the hypotheses that availability of habitat components explains relative abundance of nesting band-tailed pigeons and known nest site locations in the central Coast Range of Oregon.

## Methods

### Study Area

We conducted the study in the central Coast Range province (Franklin and Dyrness 1988) of Oregon. The study area extended approximately from Lincoln City south to Reedsport along the Pacific Coast and east to the western edge of the Willamette Valley (50 × 139 km) (Figure 1). Climate is maritime (Loy et al. 1976) and elevation varies from sea level to 1,249 m.

The Coast Range province is dominated by dense, potentially long-lived (>500 yr), coniferous forests. Two natural forest communities or distinctive vegetation zones are present: coastal sitka spruce (*Picea sitchensis*) along the western one-third of the province, and western hemlock (*Tsuga heterophylla*) along the eastern two-thirds (Franklin and Dyrness 1988). Most natural forested areas have an overstory dominated by western hemlock, western redcedar (*Thuja plicata*), Douglas-fir, sitka spruce, and red alder (*Alnus rubra*). In areas managed for timber production, which is most of the study area, the dominant tree is Douglas-fir.

The Coast Range province comprises mostly privately owned lands and public lands administered by the USDA Forest Service and the USDI Bureau of Land Management. The majority of the study area (56%) was privately owned. Land use was primarily intensive timber production on both public- and private-owned lands. An extensive network of primitive roads permeates the study area and are used primarily for timber harvest. Landscape patterns have been largely shaped by human induced disturbances (timber harvest and reforestation) (Hansen et al. 1991).

### Point Counts

We used point counts to index the abundance of band-tailed pigeons at 323 sample points (Figure 2) between 16 June and 16 August annually during 1996–1998. We considered counts of calling pigeons at sample points to estimate relative

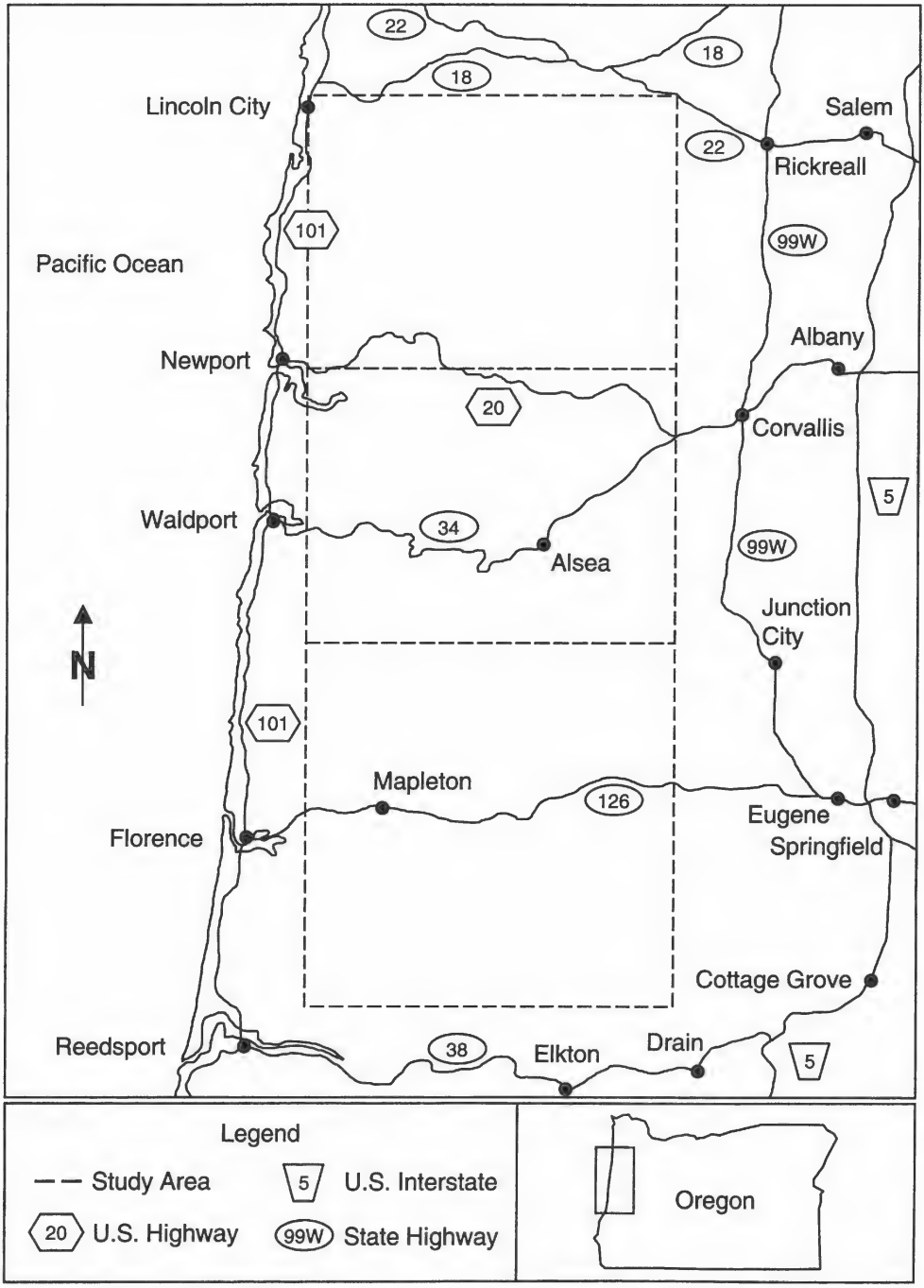


Figure 1. Location of the study area (50 × 139 km) and subareas (north, central, and south) in Oregon.

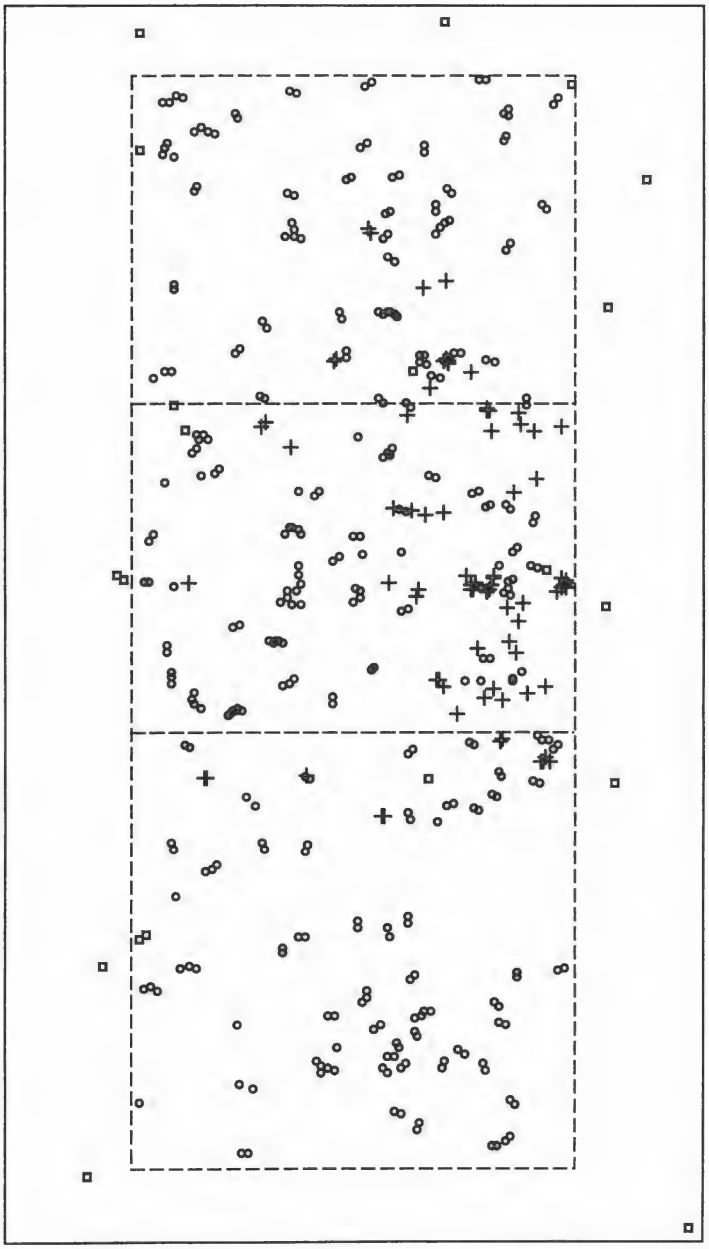

Figure 2. Distribution of 323 sample points (○), 20 known mineral sites (□), and 97 known nest sites (+) within the study area, or in the case on mineral sites, were the closest mineral source to part of the study area.

abundance of breeding males (Keppie et al. 1970, Bull 1981). Point counts were conducted beginning 10 min before official local sunrise and lasted 1 hr during mornings with <11 km per hr wind and little or no precipitation. We did not knowingly count the same pigeon more than once. We recorded the azimuth to each call to distinguish individual pigeons. Calls were considered to be of different birds when the audibility or azimuth were evidently unique, although a pigeon that obviously called from multiple locations was recorded as one.

We trained observers for 1 wk prior to surveying to increase accuracy of detections and minimize observer variability (Kepler and Scott 1981). We distributed each observer's effort equally among sample points to avoid systematic observer bias. Sample points were distributed among equal-sized subareas (north, central, and south) of the study area. Subareas were surveyed on a 1-wk rotational schedule; surveys were restricted to one subarea during a week.

We paired sample points 800 m apart for logistic reasons, and located them using a systematic, random procedure. The distance between sample points was determined so that it maximized sample size, transportation efficiency, and observer safety, while maintaining sample independence. The maximum audible range of the band-tailed pigeon coo-call for the study area was determined to be <400 m in most all forest environments (Sisson 1968, Keppie et at. 1970). We located paired sample points by generating a random location within the study area with the constraint that the site was on forested land. The location was temporarily marked on a USGS 7.5 Minute Quadrangle map (scale 1:24,000) and a second location, the first sample point, was marked at the closest point on an accessible road. A third location, the second sample point, was marked 800 m from the first sample point on an accessible road. A clear plastic overlay with concentric rings at 100-m intervals was used to find sample point locations on the nearest accessible road; either the closest point from the initial random point or 800 m from the first sample point. In cases where multiple locations were possible for the second sample point, either on the same or a different road, we systematically selected the point farther along the road of initial access and that provided the shortest driving distance between the two sample points.

## Geographic Information

We used ARC/INFO version 7.2 (Environmental Systems Research Institute, Redlands, California) to generate four themes, one raster based grid (potential nesting and feeding areas) and three vector based coverages (mineral site, sample point, and nest site), and to estimate spatial measures. The potential nesting and feeding areas theme was produced from 1988 and 1995 Thematic Mapper Imagery processed by the Coastal Landscape Analysis and Modeling Study at the Forestry Sciences Laboratory at Oregon State University to include 12 land cover types (open, water, semi-closed, broadleaf, and four tree sizes each for conifer and mixed conifer-broadleaf forest types) and was digitally referenced in 25-m pixels. The map had 98% accuracy within one land cover type and 80% accuracy overall.

The potential nesting and feeding areas theme included an area 5,000 m beyond the study area boundaries. We reclassified land cover data to represent potential nesting and feeding areas. Potential nesting area included conifer and mixed conifer-broadleaf forest with >70% canopy cover (Leonard 1998). Potential feeding area included cover types with ≤70% canopy cover (Leonard 1998). The two habitat components were mutually exclusive, and excluded only broadleaf forest with >70% canopy cover and open water cover types. Data were filtered using a majority procedure to increase the minimum mapping unit to 32 pixels (2 ha) so that there were no patches <2 ha. This procedure reduced polygon numbers and processing time in later analyses. Overall map accuracy was 97% based on visits to 154 randomly selected sites. We produced the mineral site theme from location coordinates of mineral sites known to be used by band-tailed pigeons in western Oregon during 1996–1998 (Sanders and Jarvis 2000). We produced the sample point theme from coordinates of sample points. The nest site theme was produced from coordinates of nest sites collected during a previous study (1994–1996) (Leonard 1998) that occurred within a portion of our study area.

We calculated the availability of potential nesting and feeding area, and mineral sites for the entire study area, at the sample points used to index pigeon abundance, and at known nest sites from the geographic information themes. To estimate habitat component availability at point

locations, we calculated the percentage of potential nesting area in 0.5-km radius (79 ha) plots and potential feeding area in 5-km radius (7,854 ha) plots centered on the same sample points and known nest sites using an automated macro language program. We selected plot sizes *a priori* given home range size and average travel distance of 5 km between nesting and feeding sites (Leonard 1998). The procedure consisted of (1) converting the potential nesting and feeding areas theme from a grid to a polygon coverage, (2) generating a circular plot around sample points or nests, (3) overlaying plots on the potential nesting and feeding areas coverage (having the effect of a cookie cutter; dissecting habitat polygons along plot edges, where habitat polygons outside buffers are eliminated), and (4) calculating total area of potential nesting and feeding areas. Area estimates were converted to percentage of the circular plot. We ran the procedure for each plot size. Also, we determined the straight line distance to the nearest mineral site for each sample point and nest.

To verify that areas classified as potential feeding areas had a high probability of containing food items, we visited 126 randomly selected forest areas with ≤70% canopy cover between 8 July and 5 August 1997 to determine the presence or absence of red elder, blue elder, and cascara. These shrubs rarely occur in closed-canopy forests, and produce few or no berries in such environments (Klinka et al. 1989, Randall et al. 1990).

### Statistical Analyses

We used a multiple regression model to assess the relationship between relative pigeon abundance and availability of habitat components at sample points. The response variable, pigeon abundance, tended to be skewed to the right and more uniform than predicted by normal and Poisson distributions. Fitted regression and Poisson regression models had either 8% of the residuals ≥3 units in magnitude or extra Poisson variation. However, coefficients and their standard errors are robust to non-normal distributions while deviance chi-square tests for extra Poisson variation are unreliable given means <5 (Ramsey and Schafer 1997). Consequently, we also fit a Poisson log-linear multiple regression model. The standard and Poisson log-linear regression models produced similar parameter estimates and associated *P*-values; therefore, we present statistics from the standard regression model. Similarly, a multiple linear regression model was used to assess relative pigeon abundance among 3 equal-sized subareas (west, central, and east) of the study area. We included an indicator variable in all regression models to account for seasonal differences in pigeon detections for point counts conducted during 16 June–24 July and 25 July–16 August (Sanders 1999). We used $P = 0.05$ and interaction and quadratic terms were included in models initially, then were removed when *P*-values exceeded 0.05.

We used two-sample t-tests (two-tailed) and $P = 0.05$ to compare differences in availability of habitat components between 70 successful and 27 unsuccessful band-tailed pigeon nests observed by Leonard (1998). Nests were considered successful if at least one young fledged from the nest.

## Results

The mean number of band-tailed pigeons ($2.52 \pm 0.13$) detected during 106 point counts during 16 June–24 July was 1.5 times higher than during 25 July–16 August ($1.69 \pm 0.17$) (n = 217). The probability of detecting at least one band-tailed pigeon during a 1 hr point count at sample points was 0.83 for the first survey period and 0.65 for the second survey period. Pigeon abundance varied from west-to-east, however, decreasing by 62% from the west-to-east one-third of the study area during both survey periods combined. The probability of detecting at least one pigeon during a 1 hr point count at sample points within each one-third of the study area from west-to-east was 0.88, 0.82, and 0.79 during the first survey period and 0.75, 0.76, and 0.50 during the second survey period.

We located 20 mineral sites currently used by band-tailed pigeons that were either within the study area or were the closest mineral source to part of the study area (Figure 2). The maximum distance to the closest known mineral site from any part of the study area was 37 km, but 91% of the study area was within 25 km of the nearest known mineral site. Potential nesting and feeding areas comprised 66 and 18% of the study area.

Availability of habitat components (known mineral sites and potential nesting and feedings areas) around sample points reflected availability within the study area (Figure 3). Mean potential nesting area within 0.5 km of sample points

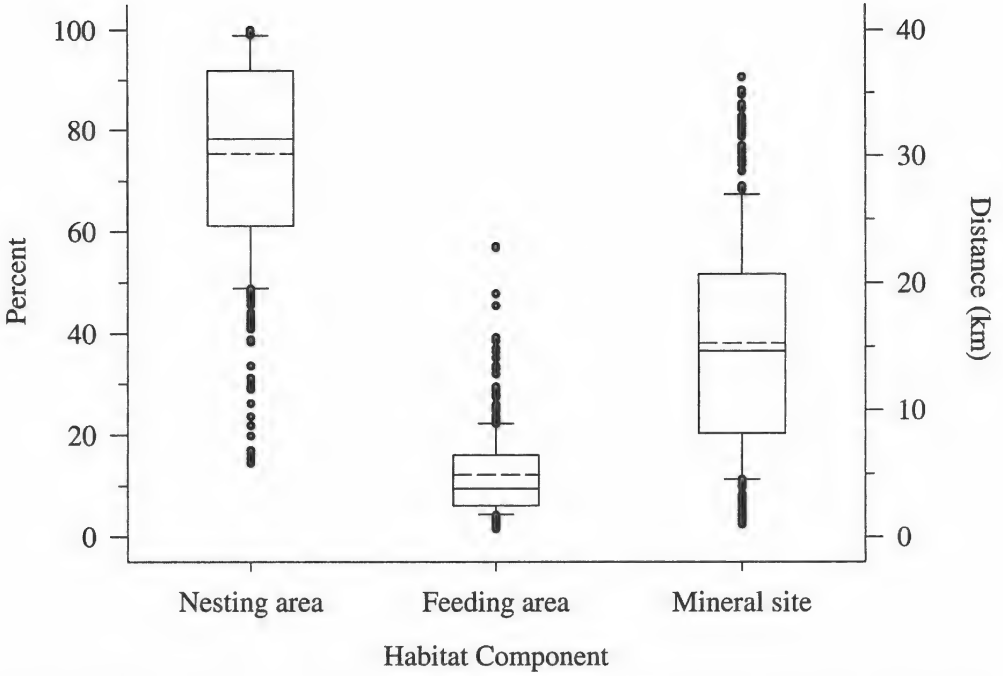


Figure 3. Distribution of 323 sample points by percent of potential band-tailed pigeon nesting and feeding areas (in 0.5-km and 5-km radius plots, respectively) and distance to nearest known mineral site in the central Coast Range of Oregon, 1995. Boxes represent the 25th and 75th percentiles, solid horizontal lines mark the value of the 50th percentile, broken horizontal lines indicate the mean, capped bars signify the 10th and 90th percentiles, and symbols mark all data outside the 10th and 90th percentiles.

was 75 ± 1.1%, mean potential feeding area within 5 km of sample points was 12 ± 0.5%, and mean distance to nearest known mineral site was 15.3 ± 0.5 km. Most (80%) of the sample points ranged from 49 to 99% (393 to 1,728 ha) potential nesting area within 0.5 km and from 5 to 22% (38 to 78 ha) potential feeding area within 5 km, and were 5–27 km of the nearest known mineral site.

Relative abundance of band-tailed pigeons at sample points was weakly related to the availability of habitat components ($P < 0.01$, $r^2 = 0.07$). Pigeon abundance decreased with increasing feeding area at sample points ($b_2 = -0.04 \pm 0.01$, 95% CI = –0.07 to –0.01, $P < 0.01$), but did not change significantly with increasing potential nest area and distance to nearest known mineral site.

Mean availability of habitat components at known nest sites did not differ significantly by nest fate; therefore, we pooled data for successful and unsuccessful nests. The availability of habitat components around known nest sites (Figure 4) resembled availability of habitat components around sample points (Figure 3), except that known nest sites tended to be closer to known mineral sites. Average nesting area within 0.5 km of nest sites was 81 ± 2.0%, average feeding area within 5 km of sample points was 16 ± 1.1%, and mean distance to nearest known mineral site was 9.6 ± 0.5 km. Most (80%) of the known nest sites had from 51 to 100% (40 to 80 ha) potential nesting area within 0.5 km, from 3 to 36% (236 to 2,827 ha) potential feeding area within 5 km, and were within 5–16 km of the nearest known mineral site.

Forested areas with ≤70% canopy cover, classified as potential feeding area, had high probability (0.80) of containing food items (berries of red elder, blue elder, or cascara) (Figure 5). Occurrence of each species, however, depended on geographic location. Red elder was most abundant along the western one-third of the Coast

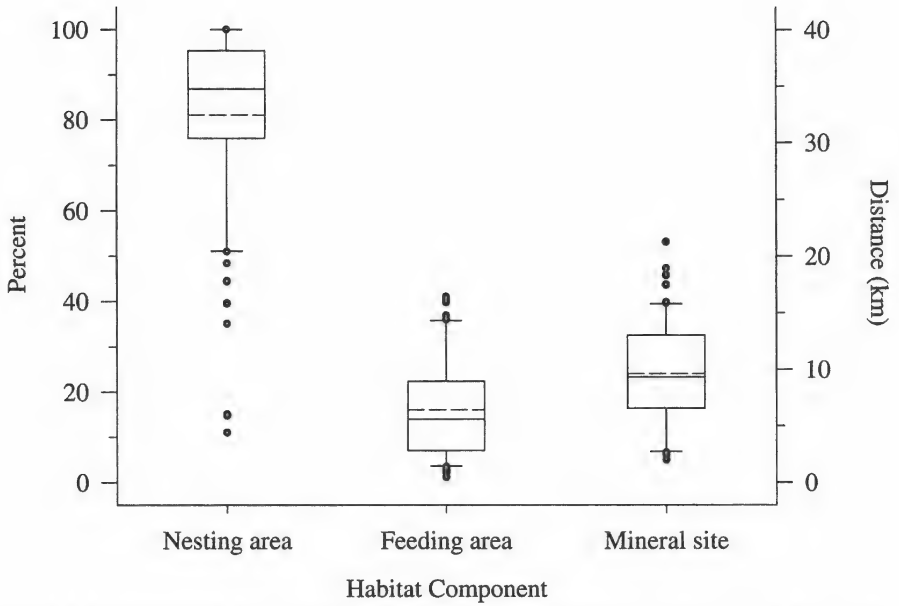


Figure 4. Distribution of 97 known nest sites by percent of potential band-tailed pigeon nesting and feeding areas (in 0.5-km and 5-km radius plots, respectively) and distance to nearest known mineral site in the central Coast Range of Oregon, 1995. Boxes represent the 25th and 75th percentiles, solid horizontal lines mark the value of the 50th percentile, broken horizontal lines indicate the mean, capped bars signify the 10th and 90th percentiles, and symbols mark all data outside the 10th and 90th percentiles.

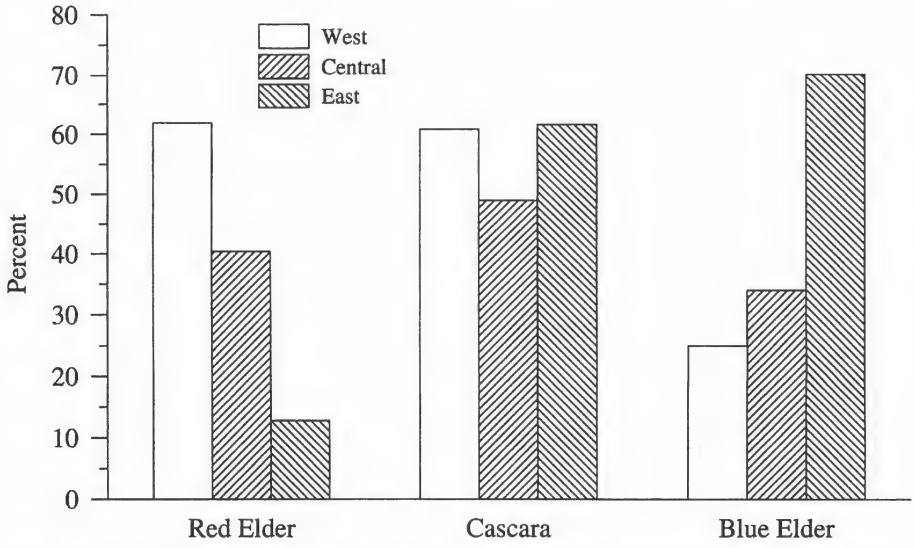


Figure 5. Percent of 126 randomly selected forested areas with ≤70% canopy cover by that contained red elder, cascara, and blue elder within equal-sized subareas (west, central, and east, n = 42 each) of the study area in the central Coast Range of Oregon, 1997.

Range, blue elder was most abundant along the eastern one-third, and cascara was most abundant along the western and eastern one-third of the study area (Figure 5).

## Discussion

Band-tailed pigeons were ubiquitous within the study area, and were detected at 83% of sample points between mid-June and late July. This result may be attributed to the prevalence and interspersion of habitat components across the central Coast Range of Oregon (Figures 3 and 4) and high mobility of pigeons. Leonard (1998) reported band-tailed pigeons in the same area had a mean breeding home range of 11,121 ha (range = 314–180,000), and traveled a mean distance of 5.0 km (range = 0.3–51.6) to feeding sites and 8.4 km (range = 3.5–14.0) to mineral sites from nest locations. Pigeons visit mineral sites about once per week (Jarvis and Passmore 1992), and are apparently capable of making flights >27 km while nesting.

We found no biologically meaningful relationship between relative band-tailed pigeon abundance and availability of habitat components (known mineral sites and potential nesting and feeding areas) within the central Coast Range of Oregon. Pigeon abundance decreased significantly with increasing potential forage area, however, this relationship was weak and did not appear biologically meaningful. Explanatory variables in the fitted model explained only 7% of the variation in relative pigeon abundance at sample points, and the estimated change in pigeon abundance was inverse to what we hypothesized. Also, potential nesting and feeding areas were mutually exclusive categories and together accounted for 84% of the study area. If band-tailed pigeon abundance increased with decreasing forage area, this implies that band-tailed pigeon abundance should have increased with increasing nest area, and there was no evidence to support that relationship.

Our results of no relationship between relative pigeon abundance and habitat component availability at sample points are seemingly conclusive. The distributions of habitat components around known nest sites were similar to the distribution of habitat components around randomly selected sample points. Nest sites were closer to known mineral sites than sample points, but this resulted from differences in study areas. Leonard's (1998) study area occurred in a portion of our study area where the maximum distance to a known mineral site was <25 km, as compared to 37 km for our study area. Thus, known nest sites did not differ from random locations based on the spatial scales and parameters we examined.

Forest areas with ≤70% canopy cover had high probability (0.80) of containing red elder, blue elder, or cascara berries, however, occurrence of each species depended on longitudinal position within the Coast Range (Figure 5). Kozloff (1976) noted the two kinds of elder did not often mix; red elder grows best near the coast in wet habitats, whereas blue elder inhabits dryer areas and is a more common species along the eastern edge of the Coast Range. Although open-canopied forest areas represent potential feeding areas for band-tailed pigeons, longitudinal position within the study area and plant species phenology influence actual food availability.

West-to-east variation in band-tailed pigeon abundance was correlated with the apparent availability of red elder and cascara within potential feeding sites, but also coincided with a number of confounding natural and induced landscape patterns. The study area naturally varied from west to east in climate and vegetation (Franklin and Dyrness 1988, Loy et al. 1976). Gabrielson and Jewett (1940) reported band-tailed pigeons in Oregon reach greatest abundance along the coast. Food for nesting pigeons is most available along the coastal side of the Coast Range and least available along the inland side, especially when we conducted our study.

The extent to which the distribution and berry production of elder and cascara has changed over time and the effect on band-tailed pigeon populations is unknown. Elder and cascara shrubs are prevalent in early to intermediate forest successional stages, are prolific producers of berries, and appear to be abundant. However, little is known about the autecology of these species. Factors that can affect the availability of these food resources include: 1) herbicide application following intensive harvest (Hansen et al. 1991); 2) harvest for medicinal use (Starker and Wilcox 1931); and 3) clearing for agricultural practices (Starker and Wilcox 1931). Although the overall distribution of elder and cascara has not likely changed, the

volume of berry production most likely has changed in relation to shrub number, size, form, and overstory shading.

Band-tailed pigeons are widely distributed across the central Coast Range of Oregon, with abundance decreasing from west to east; however, the cues by, and scales at which these birds select breeding habitat is unknown. Decreasing abundance of breeding Pacific Coast band-tailed pigeons over two to three decades does not appear related to availability of potential nesting and feeding areas and known mineral sites, but may be related to actual food availability. Further study is needed to understand the relationship between food availability and pigeon abundance in western Oregon.


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## Literature Cited


Braun, C. E. 1994. Band-tailed pigeon. Pages 60-74 *In* T. C. Tacha and C. E. Braun (editors), Migratory shore and upland game bird management in North America. International Association of Fish and Wildlife Agencies, Washington, D.C.

Bull, E. L. 1981. Indirect estimates of abundance of birds. Studies in Avian Biology 6:76-80.

Franklin J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis, Oregon.

Gutiérrez, R. J., C. E. Braun, and T. P. Zapatka. 1975. Reproductive biology of the band-tailed pigeon in Colorado and New Mexico. Auk 92:665-677.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience 41:382-392.

Hansen, A. J., S. L. Garman, and B. Marks. 1993. An approach for managing vertebrate diversity across multiple-use landscapes. Ecological Applications 3:481-496.

Harris, L. D. 1984. The Fragmented Forest. University of Chicago Press, Chicago, Illinois.

Jarvis, R. L., and M. F. Passmore. 1992. Ecology of band-tailed pigeons in Oregon. Biological Report 6, USDI Fish and Wildlife Service, Washington D.C.

Keppie, D. M., H. M. Wight, and W. S. Overton. 1970. A proposed band-tailed pigeon census—a management need. Transactions of the North American Wildlife and Natural Resources Conference 35:157-171.

Kepler, C. B., and J. M. Scott. 1981. Reducing bird count variability by training observers. Studies in Avian Biology 6:366-371.

Klinka, K., V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. Indicator plants of coastal British Columbia. University of British Columbia Press, Vancouver, British Columbia, Canada.

Kozloff, E. N. 1976. Plants and animals of the Pacific Northwest: an illustrated guide to the natural history of western Oregon, Washington, and British Columbia. University of Washington Press, Seattle, Washington.

Leonard, J. P. 1998. Nesting and foraging ecology of band-tailed pigeons in western Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Loy, W. G, S. Allan, and C. P. Patton. 1976. Atlas of Oregon. University of Oregon Books, Eugene, Oregon.

March, G. L., and R. M. F. S. Sadleir. 1972. Studies on the band-tailed pigeon (*Columba fasciata*) in British Columbia. II. Food resources and mineral-gravelling activity. Syesis 5:279-284.

Neff, J. A. 1947. Habits, food, and economic status of the band-tailed pigeon. North American Fauna 58, USDI Fish and Wildlife Service, Washington, D.C.

Pabst, R. J., and T. A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. Canadian Journal of Botany 76:298-315.

Ramsey, F. L., and D. W. Schafer. 1997. The Statistical Sleuth. Duxbury Press, Belmont, California.

Randall, W. R., R. F. Keniston, D. N. Bever, and E. C. Jensen. 1990. Manual of Oregon Trees and Shrubs. Oregon State University Book Stores, Corvallis, Oregon.

Sanders, T. A. 1999. Habitat availability, dietary mineral supplement, and measuring abundance of band-tailed pigeons in western Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Sanders, T. A., and R. L. Jarvis. 2000. Do band-tailed pigeons seek a calcium supplement at mineral sites? Condor 102:855-863.

Sisson, L. H. 1968. Calling behavior of band-tailed pigeons in reference to a census technique. M.S. Thesis, Oregon State University, Corvallis, Oregon.

Spies, T. A., J. Tappeiner, J. Pojar, and D. Coates. 1991. Trends in ecosystem management at the stand level. Transactions of the North American Wildlife and Natural Resources Conference 56:628-639.

Starker, T. J., and A. R. Wilcox. 1931. Cascara. American Journal of Pharmacy 103:73-97 and 103:147-175.

Tappeiner, J. C., D. Lavender, J. Walstad, R. O. Curtis, and D. S. DeBell. 1997. Silvicultural systems and regeneration methods: current practices and new alternatives. Pages 151-164 *In* K. A. Kohm and J. F. Franklin (editors), Creating a forestry for the 21st century. Island Press, Washington, D.C.

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*Accepted for publication 21 April 2003*

Verner, J. 1981. Measuring responses of avian communities to habitat manipulation. Studies in Avian Biology 6:543-547.

Western Migratory Upland Game Bird Technical Committee. 1994. Pacific Flyway management plan for the Pacific Coast population of band-tailed pigeons. Pacific Flyway Council, USDI Fish and Wildlife Service, Portland, Oregon.

Wiens, J. A. 1989. The Ecology of Bird Communities: Volume 2. Processes and Variations. Cambridge University Press, Cambridge, United Kingdom.

Wiens, J. A., and J. T. Rotenberry. 1981. Censusing and the evaluation of avian habitat occupancy. Studies in Avian Biology 6:522-532.

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# Bird Communities in Oak Woodlands of Southcentral Washington

## Abstract

This study was initiated because there was a perception that oak woodlands are unique habitats for birds, particulary Neotropical migrants. The objectives of this study were to determine species composition and relative abundance of bird populations in oak and oak-conifer woodlands; and to evaluate the importance of these habitats to nesting birds. This study was undertaken near the northern limit of the Garry oak habitat in North America. The study design consisted of three replicates each of five upland habitats and three riparian habitats. Seventy-two bird species (53 Neotropical migrants and 19 permanent residents) were found at least twice on the 18 study sites. There were no significant differences in species richness among upland habitats. An average of 12 neotropical migrant species were detected per study site in both upland and riparian areas. Neotropical species comprised 62% of all birds detected. Bird abundance was highest in study sites with large amounts of small oak and small pine; it was lowest in riparian study sites. The most abundant species was the Nashville warbler. Bird species composition in the Washington Garry oak habitat was different from those previously reported from Oregon and California.

## Introduction

Among the factors likely to cause avian or other wildlife population declines, habitat loss and modification are two of the most important. Birds strongly associated with limited habitats have a higher potential for population decline than those affiliated with more widespread habitats. Furthermore, animals at the fringes of their distributions have less stable populations (Caughley and Sinclair 1994). The Garry oak (*Quercus garryana*) habitat has been threatened by encroachment of conifer species, firewood cutting, and livestock grazing. There has been concern that this habitat is critical for birds and other organisms and its loss would cause significant population declines in some oak-dependent birds (DeGroot et al. 2000). In California, tan oak (*Lithocarpus densiflorus*), coast live oak (*Q. agrifolia*), and California black oak (*Q. kelloggii*) have been decimated by a new disease referred to as Sudden Oak Death, an undescribed *Phytophthoia* fungus (Svihra et al. 2001), and Garry oak may become a new host. Therefore, understanding the ecology of the Garry oak community is now more important than ever.

This study was initiated, in part, because there was a perception that oak woodlands are unique habitats for birds. Klickitat County contains the most extensive examples of oak woodlands remaining in Washington, where large areas of oaks exist either in pure patches or mixed with conifers. Ornithologically, oak woodland habitat appears to differ from other habitats in Washington in two ways. First, bird species diversity is high compared with coniferous forests (Manuwal 1991). Second, it provides the primary nesting habitat for oak woodland specialists: the acorn woodpecker (*M. formicivorus*), ash-throated flycatcher (*Myiarchus cinerascens*), and western scrub jay (*Aphelocoma californica*). Of these three species, the western scrub jay may be the most common. The acorn woodpecker is limited to a small colony near Lyle, Washington, at the mouth of the Klickitat River. The ash-throated flycatcher is found in various locations in southern Washington from about Bingen eastward where it is primarily found among oaks (Seavey 1997). Washington represents the northern edge of its breeding distribution since it is accidental in British Columbia (Campbell et al. 1997).

Several papers describe the bird communities of oak woodlands in California (Verner and Ritter 1985, Verner 1987, Avery and Van Ripper 1989, Block et al. 1994, Aigner et al. 1998) and Oregon (Anderson 1970a, 1970b, 1972; Sterns 1995). There are no published accounts of bird communities associated with oaks in Washington.

The Garry oak community, found in Oregon and parts of northern California, extends north into western and south-central Washington. Oak woodlands are patchily distributed in western Washington. Oak woodlands remain in the Fort Lewis area, although they are threatened by human encroachment, invasion by alien plant species

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and a history of fire suppression (Tveten and Fonda 1999). Thus, the extensive oak and oak-conifer forests in south-central Washington represent the largest examples of oak woodland habitat in Washington. The Klickitat and White Salmon drainages are in the heart of this region. Garry oak may be found mixed with either Douglas-fir (*Pseudotsuga menziesii*) or ponderosa pine (*Pinus ponderosa*) in south-central Washington. Of particular importance is the Garry oak woodland community and its ecotone with the ponderosa pine woodland, a habitat characteristic of most of the lower east slope of the Washington Cascades (Franklin and Dyrness 1988). Oak and oak-conifer habitats provide habitat for birds such as the western scrub jay, that are uncommon elsewhere in Washington. Characteristics of the bird communities of oak woodlands in south-central Washington are poorly known, and little is known about the value of these woodlands to Neotropical bird species. The objectives of this study were to (1) determine species composition and relative abundance of bird populations in oak and oak-conifer woodlands, and (2) evaluate the importance of these habitats to nesting Neotropical migrants.

## Study Area

The study was conducted at three primary geographical locations in south-central Washington: 1) the White Salmon River, 2) the Klickitat River, and 3) areas near Goldendale (Figure 1). The study site represented mixes of oak and conifers and successional age classes. The habitats were selected on their general appearance because they represented the variation that existed within the oak woodlands in south-central Washington. The upland areas were divided into the following general types with three replicates per habitat: large pine-large oak (LP-LO); small pine-small oak (SP-SO); large Douglas-fir-large oak (LF-LO); mostly pure large oak (LO); and mostly pure small oak (SO). The Klickitat Oak Mapping Inventory of the Washington Resource Data System (WRDS), a GIS data bank, provided by the Washington Department of Fish and Wildlife (WDFW), was helpful in selecting some study areas.

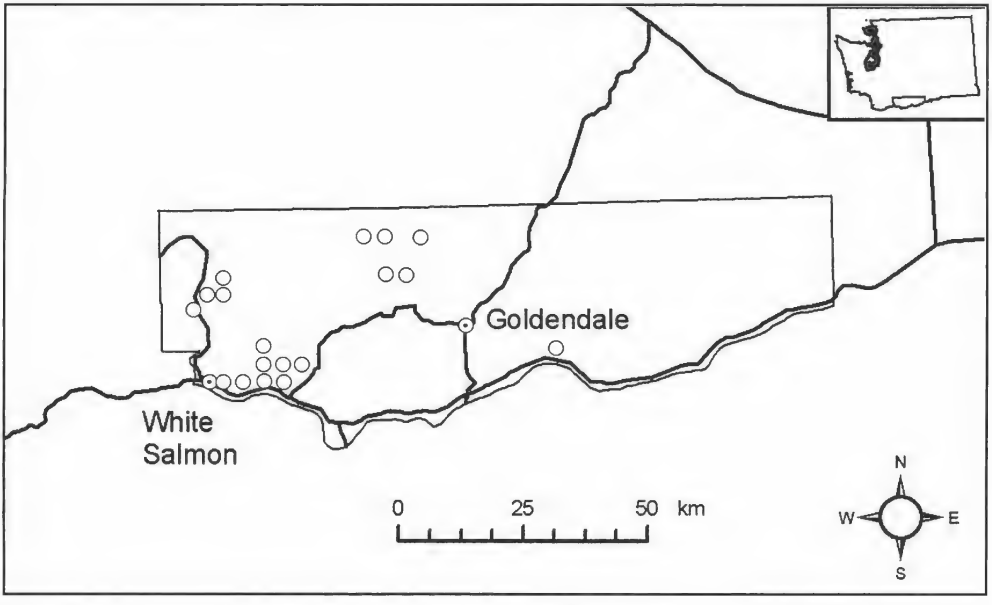


Figure 1. Location of study sites in oak woodland habitat in south-central Washington.

## Methods

### Field

The field crew surveyed five upland habitats with three replicates in each habitat (n = 15), and three riparian areas (n = 3). The fixed radius point count method (Verner 1985, Manuwal and Carey 1991) was used to obtain an index of bird abundance. In each of the selected study sites, an array of 10 points spaced 100 m apart and at least 50 m from the study site edge (except riparian study sites) was used to determine abundance, species richness, and species composition. We selected the largest accessible study sites that were representative of a particular habitat. Nevertheless, some individual study sites were in habitat patches that did not allow point count stations to be spaced more than 100 m apart. A bird survey consisted of tallying all individual birds heard or seen near each point for 8 min. Surveys usually began within 15-30 min of official dawn. In 1995 and 1996, five surveys were made at each study site, beginning in late April and ending at about 7 July.

All vegetation was sampled at the 10 bird point count locations. At each point, the number and dbh of trees and snags were counted in a 13-m-radius (0.05 ha) circular plot. Tree species composition was determined from the 13-m-radius circular plot data.

### Data Analysis

I calculated the total number of birds detected to compare bird abundance among different habitats. Birds detected in a study site only once were omitted from the analysis since those birds were probably either migrants moving through or vagrant non-breeding birds and therefore were not representative of the study sites. I also calculated the total number and mean number of species detected per study site and then obtained the average for a habitat. One-way Analysis of Variance (ANOVA) was used to compare differences in species richness and total detections among habitats. Square-root transformed mean number of detections and mean number of species were used as the variables. SPSS v11 was used in performing statistical tests. The level of significance for each analysis was $P = 0.05$. I used the Jaccard's similarity index (Ijs = species in common/all species x 100) ( Muller-Dombois and Ellenberg 1974) to compare regional bird communities. By using the percentage tree composition for each study site, I calculated the Shannon-Weaver index $H' = -p_i \log_e p_i$, where $p_i$ is the proportion of individuals in the ith tree species (Shannon and Weaver 1963) as a simple measure of tree species diversity.

## Results

### Description of Habitats

The LP-LO habitat was characterized by widely-spaced large diameter Garry oak and ponderosa pine, and some bigleaf maple (*Acer macrophyllum*) in the Columbia Gorge area (Table 1). Understory shrubs were also widely scattered, although there

TABLE 1. Percent composition of live trees and mean diameter at breast height (cm) (in parentheses) of live trees and snags in six habitats in south-central Washington in 1995. Snags were treated as a species in calculation of the diversity index.

| Tree species | Large pine-large oak (n = 553) | Small pine-small oak (n = 1028) | Large fir-large oak (n = 388) | Pure large oak (n = 387) | Pure small oak (n = 1168) | Riparian (n = 1092) |
|---|---|---|---|---|---|---|
| Garry oak | 73.3 (16.5) | 80.7 (10.1) | 45.6 (21.9) | 98.4 (21.4) | 95.1 (10.4) | 67.0 (18.8) |
| Ponderosa pine | 6.6 (30.5) | 18.6 (20.5) | | 1.3 (34.3) | 2.7 (26.3) | 4.6 (34.4) |
| Douglas-fir | | 0.7 (30.3) | 28.3 (25.1) | 0.3 | 2.2 (9.9) | 0.3 (37.9) |
| Grand fir | | | 14.1 | | | |
| Bigleaf maple | 20.1 (7.0) | | 9.8 (12.3) | | | 2.5 (19.7) |
| Red alder | | | 2.2 | | | |
| Cottonwood | | | | | | 1.7 (49.1) |
| Oregon ash | | | | | | 2.3 (15.9) |
| Garry oak snag | 46.4 | 15.9 | 18.8 | 18.1 | 8.0 | 21.5 |
| Ponderosa pine snag | | | | | | 18.5 |
| Cottonwood snag | | | | | | 34.4 |
| Unidentified snag | | | | | | 43.0 |
| Diversity (H') | 0.81 | 0.60 | 1.46 | 0.17 | 0.42 | 1.31 |

were occasional clumps. The mean height of Garry oak was 9 m, ponderosa pine 10 m, and bigleaf maple 6 m.

The SP-SO habitat had a high density of small diameter, often clumped Garry oak. Larger diameter and taller ponderosa pine were mixed with the oak. Mean tree heights were Garry oak 7 m, ponderosa pine 11 m, and Douglas-fir 13 m.

The LF-LO habitat was only found in the White Salmon drainage west of the other study areas. Mean tree heights were grand fir (*Abies grandis*) 17 m, Douglas-fir 14 m, Garry oak 13 m, bigleaf maple 10 m.

LO study sites were in the White Salmon area and along the Columbia Gorge. The only trees species present were Garry oak (mean height 10 m), ponderosa pine 6 m, and a single Douglas-fir in one study site. These study sites were open with little understory.

Study sites of SO contained high densities of small diameter Garry oak with either Douglas-fir or large ponderosa pine scattered through the study site (Table 1). Mean height for oak was 7 m, ponderosa pine 12 m, and Douglas-fir 8 m.

Riparian vegetation was highly variable and contained more tree species than the upland study sites (Table 1). Garry oak and black cottonwood (*Populus trichocarpa*) were the most common species, making up 80% of all trees. Other tree species included ponderosa pine, Oregon ash (*Fraxinus latifolia*), bigleaf maple, red alder (*Alnus rubra*), cottonwood snags, and oak snags.

Highest tree species richness occurred in LF-LO and riparian areas (Table 1). The LF-LO study sites (in the White Salmon drainage) consisted of 43% Garry oak, 27% Douglas-fir, 13% grand fir, and 9% bigleaf maple. These species made up 92% of all the trees. Riparian areas had more species, but Garry oak constituted 64% of the total trees present. The next most abundant species was cottonwood, which constituted 12% of the total. Lowest tree species richness was found in LO study site (Table 1), which consisted of large widely-spaced oaks making up 97% of the tree species present.

Snags were not a prominent feature of any of the study sites, accounting for only 2% of all trees sampled. The largest percentage of snags occurred in LF-LO study sites (5%) and riparian study sites (4%), but the largest number and largest diameter snags occurred in riparian areas. There was little deadwood on the ground in most study sites. Despite the general lack of snags and forest floor woody debris, dead branches and holes in the trunk were characteristic of most Garry oaks in the study site. These characters increased with the age of the tree.

## Avian Species Composition and Richness

There were 53 species of Neotropical migrants and 19 species of permanent residents detected in the 18 study sites during 1995 and 1996. Seventy-two bird species were detected more than once in 1995 or 1996 in the 15 upland study sites. Mean number of species detected per study site was 21 $\pm$ 0.94 (Figure 2). Species composition varied somewhat among the various study sites. There were no significant differences in species richness among upland habitats. The large amount of variation among study sites probably masked any possible significant differences. The total species detected in each habitat were LP-LO (52), SP-SO (40), LF-LO (48), LO (58), SO (55), and riparian (64).

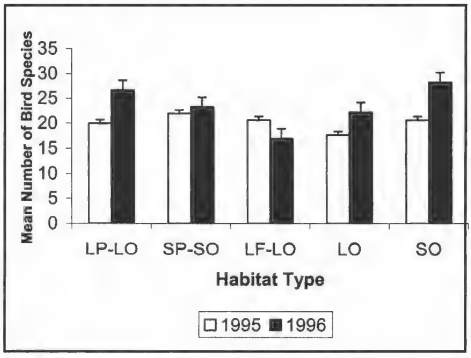


Figure 2. Number of bird species and standard error at upland (n = 15) oak woodland study sites in south-central Washington, 1995-1996.

In the three riparian study sites, the mean number of bird species detected per study site was 25 for both years. The warbler (10 species) and flycatcher (6 species) groups contained the largest number of species. A complete summary of relative abundance by species in each habitat is available from the author.

## Avian Abundance

We detected over 6,200 individual birds within the 50 m radius of the point count stations over the 2 yr. Neotropical migrants made up 64 ±2.3 % of birds detected in the 15 upland study sites and 59 ± 3.5 % of birds detected in the 3 riparian areas (Table 2). Highest number of detections were in SP-SO, LF-LO, and SO habitats (Figure 3). Large pine-large oak and riparian areas had the lowest number of detections. There was no significant difference in birds detected between years. The dark-eyed junco (*Junco hyemalis*), Nashville warbler (*Vermivora ruficapilla*), and American robin (*Turdus migratorius*) were found at all study sites. The spotted towhee (*Pipilo maculatus*), western tanager (*Piranga ludoviciana*), chipping sparrow (*Spizella passerina*), brown-headed cowbird (*Molothrus ater*), and red-breasted nuthatch (*Sitta canadensis*) were found at 73-97% of all study sites. The yellow warbler (*Dendroica petechia*), song sparrow (*Melospiza melodia*), and olive-sided flycatcher (*Contopus cooperi*) are examples of species that were found at only 1-2 study sites.

TABLE 2. Most abundant birds in upland oak, oak-conifer woodlands and riparian areas in 1995 and 1996 in South-central Washington (top 50%). Numbers are number of detections <50 m of point count station. Percent refers to percent of all detections in either upland or riparian habitats.

| Species | Mean Total | Percent of Total |
|---|---|---|
| **Upland Habitats** | | |
| Nashville warbler | 333 | 10.6 |
| Chipping sparrow | 285 | 9.0 |
| Dark-eyed junco | 240 | 7.6 |
| Spotted towhee | 207 | 6.6 |
| Yellow-rumped warbler | 159 | 5.1 |
| American robin | 147 | 4.7 |
| Red-breasted nuthatch | 141 | 4.5 |
| Brown-headed cowbird | 124 | 3.9 |
| **Riparian Habitat** | | |
| Nashville warbler | 64 | 13.5 |
| Spotted towhee | 48 | 10.1 |
| Black-throated gray warbler | 45 | 9.6 |
| American robin | 42 | 8.9 |
| Dark-eyed junco | 34 | 7.2 |
| Vaux's swift | 23 | 4.9 |

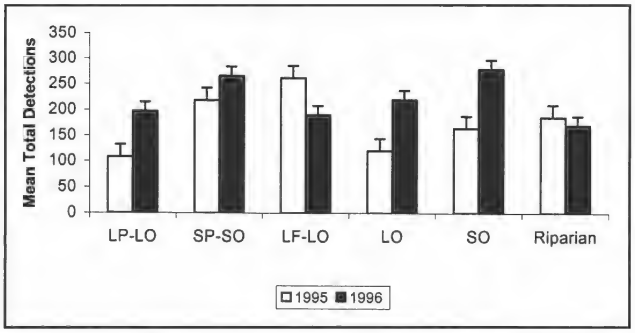


Figure 3. Total mean number of detections of upland (n = 15) and riparian (n = 3) study sites during 1995 and 1996. Means are for 3 study sites per habitat. Bars are standard error.

Neotropical migrants made up over 62% of all species detected. The highest percentages of Neotropical migrants occurred in LP-LO and SO habitats. Neotropical migrants were represented by 10 species of warblers and 7 species of flycatchers; warblers made up 21% and flycatchers 5% of 6273 detections over the 2 yr. The black-throated gray warbler (*D. nigrescens*) and Nashville warbler were the most common warblers, followed by the yellow-rumped warbler (*D. coronata*) or orange-crowned warbler (*V. celata*). Many of the yellow-rumped warblers were undoubtedly migrants and not nesting birds. The Nashville warbler was by far the most abundant nesting warbler, accounting for almost half the warbler detections.

Seven species of flycatchers were detected during this study, with differences in the number of flycatcher species between habitats and among study sites within a habitat. Flycatcher data for 1995 may contain some misidentifications because field observers were unable to distinguish some of the flycatcher species early in the season. Flycatcher species richness was lowest in the LF-LO habitat. In 1996 small numbers of Hammond's flycatcher (*Empidonax hammondi*) and Pacific-slope flycatcher (*E. difficilis*) (the most common flycatcher in LF-LO) were detected in LF-LO. The western wood-pewee (*Contopus sordidulus*) was the most common and widely-distributed of the seven species of flycatchers, absent only in LF-LO study sites.

## Discussion

Bird species richness was similar among the 15 upland sites (Figure

2), even though the sites differed in tree heights and average dbh (Table 1). This similarity was likely due to the relative lack of vertical habitat diversity, especially in the large oak stands where there were few shrubs and oak trees were widely scattered. Although species richness was similar, species composition differed, particularly in regard to the species of flycatchers and warblers. Species richness was higher in riparian sites compared with average richness in upland sites (Figure 2). High avian species richness in riparian areas was due to the generally higher habitat structural diversity along riparian areas since there were more shrubs and taller trees, and because the riparian areas we sampled were linear, thus including a substantial amount of edge within the 50-m radius circle of the point count.

Bird abundance was high in study sites dominated by a mixture of small oaks and small pines, and stands of almost pure small oak (Figure 3). These stands had large amounts of edge created by the clumping of trees and past timber harvesting. Species such as the spotted towhee, chipping sparrow, gray flycatcher (*E. wrightii*), and dusky flycatcher (*E. oberholseri*) were common in such areas. Most of these sites had a few scattered large oaks and pines that provided additional structural diversity to the sites. They provided nesting opportunities for cavity-nesting birds such as northern flicker (*Colaptus auratus*) and red-breasted nuthatch, and perch sites and nest sites for American kestrel (*Falco sparverius*).

Our riparian areas had unexpectedly fewer detections than upland sites (Figure 3). Riparian areas reportedly have higher species richness and total abundance than adjacent upland areas (Oakley, et al. 1985). The riparian areas we sampled were along streams so that the observers may have actually reduced the area they sampled by confining their detections to within the riparian vegetation zone. In many cases, the riparian width was less than the 13-m radius around point count stations. Riparian areas attracted the red-eyed vireo (*V. olivaceus*) and yellow-breasted chat (*Icteria virens*); neither were recorded in upland habitats. Some other species, such as the Vaux's swift (Table 3) and ash-throated flycatcher (Seavey 1997) tended to be more common near riparian areas.

Species richness was considerably higher in virtually all oak woodland habitats compared with any of the age classes of west-side Douglas-fir studied by Manuwal (1991). For example, mean species richness at the study site level in Douglas-fir forests ranged from 13 in mature study sites to 18 in old-growth study sites. In oak woodland upland study sites, mean species richness was 21. Seventy-two species of birds were detected in the oak woodlands study, whereas only 34 species were detected in the Douglas-fir study sites. Raptors were omitted in this comparison.

Although geographical variation complicates comparisons with studies conducted in other parts of the West, nevertheless some notion of the importance of oaks to birds can be gained by making such comparisons (Table 3). Compared to published accounts of bird communities in oak habitats of the Pacific states, only 32% of the bird species in the Washington habitats were the same as the Oregon sites and only 6% were the same as those reported from the oak-pine woodlands of central California.

A much higher percentage of the total bird community consisted of Neotropical migrants in oak woodlands than in west-side Douglas-fir

TABLE 3. Similarity (%) between Garry oak bird communities in south-central Washington and selected oak habitats in Oregon and California.

| Comparison | Garry oak south-central Washington This study | Garry oak-conifer western Oregon Anderson 1972 | Blue oak-conifer northern California Avery and Van Ripper 1989 | Oak-pine woodland central California Verner and Ritter 1985 |
|---|---|---|---|---|
| Bird species comprising top 50% of abundance (see Table 2) | 100 | 12 | 5.9 | 0 |
| All bird species in community recorded at least twice. | 100 | 31.5 | 12.0 | 18.3 |

habitat. In Douglas-fir study sites from Mt. Rainier south to the Columbia River, Neotropical migrants made up 33% of the avifauna inhabiting mature Douglas-fir forests, and 45% of young forests (Manuwal 1991). The most abundant Neotropical migrants were the Pacific-slope flycatcher, hermit-Townsend's warbler (*D. occidentalis* x *townsendi*), and dark-eyed junco. In contrast, Neotropical birds made up nearly 70% of all birds in upland oak habitat I studied. Oak woodlands provide nesting habitat for large numbers of Nashville warblers (Table 2). Densities of this species in oak woodlands may be higher than for any other habitat occupied by this species in its western range.

The oak woodlands of south-central Washington provide a diverse habitat for birds in general and for three species found exclusively or primarily in oaks. These woodlands are substantially different in species composition from other forest habitats (Table 3) and are important for several species of Neotropical birds. Highest overall bird densities and species richness occurred in areas dominated by a mixture of small oaks and pines. Fortunately, this habitat is currently common on state-owned lands, however, certain areas need to be identified and protected as part of a Neotropical bird management plan.

## Literature Cited


Aigner, P. A., W. M. Block, and M. L. Morrison. 1998. Effect of firewood harvesting on birds in a California oak-pine woodland. Journal of Wildlife Management 62: 485-496.

Anderson, S. H. 1970a. Forest birds of western Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Anderson, S. H. 1970b. The avifaunal composition of Oregon white oak study site. Condor 72:417-423.

Anderson, S. H. 1972. Seasonal variations in forest birds of western Oregon. Northwest Science 46:194-206.

Avery, M. L., and C. Van Ripper III. 1989. Seasonal changes in bird communities of the chaparral and blue-oak woodlands in central California. Condor 91:288-295.

Block, W. M., M. L. Morrison, J. Verner, and P. N. Manley. 1994. Assessing wildlife-habitat-relationships models: a case study with California oak woodlands. Wildlife Society Bulletin 22:549-561.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. E. McNall, and G. E. John Smith. 1997. The Birds of British Columbia, Vol. 111. University of British Columbia Press, Vancouver, British Columbia, Canada.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife Ecology and Management. Blackwell Scientific Publications, Cambridge, UK.



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DeGroot, K., P. Boulay, C. Macdonald, G. Fitzpatrick, K. Floe, T. Ennis, and P. Dunn. 2000. So a mighty oak can grow. Bird Conservation 14:6-7.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Manuwal, D.A. 1991. Spring bird communities in the southern Washington Cascade Range. Pages 160-174 *In* L. F.Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Manuwal, D. A., and A. B. Carey. 1991. Methods for Measuring Populations of Small, Diurnal Forest Birds. Pages 1-21 *In* A. B. Carey, and L. F. Ruggiero (editors),Wildlife-Habitat Relationships: Sampling Procedures for Pacific Northwest Vertebrates. USDA Forest Service General Technical Report PNW-GTR-278. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York.

Oakley, A. L., J. A. Colins, L. B. Everson, D. A. Heller, J. C. Howerton, and R. E. Vicent. 1985. Riparian zones and freshwater wetlands. Pages 57-80 *In* E. R. Brown (technical editor), Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. USDA

Forest Service Publication R6-F & WL-192-1985. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Seavey, J. 1997. Nest study site selection and nesting success of the ash-throated flycatcher in south-central Washington. M.S. Thesis, University of Washington, Seattle, Washington.

Shannon, C. and W. Weaver. 1963. The mathematical theory of communication. University of Illinois Press, Urbana.

Sterns, M. A. 1995. Avifauna in oak woodland habitats of the Willamette Valley, Oregon, 1994. Unpublished report on file at USDI Fish and Wildlife Service, Portland, Oregon.

Svihra, P., K. E. Keirman, N. K. Palkovsky, and A. J. Storer. 2001. Sudden oak death: an update of the facts. University of California, Davis, Cooperative Extension in Marin County, Pest Alert 4a, June 2001. Novato, California.

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Tvetan, R. K., and R.W. Fonda. 1999. Fire effects on prairies and oak woodlands on Fort Lewis, Washington. Northwest Science 73:145-158.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2:247-302.

Verner, J. 1987. Preliminary results from a system for monitoring trends in bird populations in oak-pine woodlands, Pages 214-222 *In* T. R. Plumb and N. H. Pillsbury (technical editors). Multiple-use management of California's hardwood resources. USDA Forest Service General Technical Report. PSW-100. Pacific Southwest Forest and Range Experiment Station, Fresno, California.

Verner, J., and L. V. Ritter. 1985. A comparison of transects and point counts in oak-pine woodlands of California. Condor 87:47-68.

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# A Terrestrial Arthropod Index of Biological Integrity for Shrub-Steppe Landscapes

## Abstract

We studied arthropods in shrub-steppe at the Idaho National Engineering and Environmental Laboratory to identify scientifically sound indicators of ecological condition and to develop a terrestrial index of biological integrity (T-IBI), an analog of the multimetric indexes used to manage water resources. We sampled terrestrial arthropods with pitfall traps in late spring at nine sites selected to reflect little or no human disturbance and diverse histories of human activity (livestock grazing, chemical contamination, physical disturbance, restoration). Our evaluation of 56 assemblage attributes—measured as taxa richness or the relative abundance of key taxonomic, trophic, or ecological groups—sought measures that varied systematically with human influence. From 21 attributes that did vary significantly with disturbance, we selected 8 for a T-IBI. This Idaho T-IBI correlated significantly with human influence across the nine sites. We compared this index with an independently developed T-IBI, also comprising eight metrics, from three years' study at the Hanford Nuclear Reservation in Washington State. Six metrics were identical in both indexes. Combining our Idaho and Hanford results, we propose a nine-metric T-IBI for shrub-steppe lands. Concordance of metrics and the index in two widely separated shrub-steppe environments suggests that T-IBI offers an effective means of measuring biological condition. Parallels in this terrestrial system with the extensive aquatic work applying the same principles further suggest that this T-IBI could be effective in guiding conservation and restoration decisions in shrub-steppe landscapes.

## Introduction

Human activity changes environments, sometimes in big, obvious ways, sometimes in small, subtle ways. Converting shrub-steppe to agriculture or clearcutting a forest inevitably and visibly alters the mix of plants, insects, birds, and mammals at a site. Damming, channeling, or polluting a river inevitably, but perhaps less visibly, alters the river's biota. Such biotic changes are most often documented as counts of threatened and endangered species or as declining populations or production of species with commercial or recreational value. Unfortunately, the preoccupation with imperiled and commodity species obscures wider consequences of human activity for living systems. Without a report card for those wider consequences, society cannot effectively identify and protect ecologically intact places, restore those that are degraded, or make informed decisions about permits for development.

Understanding human impacts on the living world requires well-selected indicators. Good indicators provide ecologically sound, quantitative information relevant to public policy. They represent diverse dimensions of the system under study, simplify information about complex phenomena to improve communication with interested parties, and are cost-effective (National Academy of Sciences 2000). Identifying indicators that meet these standards requires a rigorous scientific process beginning with proper study design, including appropriate sampling and analytical methods, and ending with synthesis and communication of study results (Karr and Chu 1999).

The use of multimetric biological indexes in aquatic systems—specifically the index of biological integrity (IBI)—transformed water resource programs (Davis 1999). IBI was a direct response to the Clean Water Act's 1972 mandate to restore and maintain the biological integrity of the nation's waters. The broad measurement categories included in the original IBI—taxonomic richness, species composition, trophic composition, abundance, and condition—offer robust indicators at multiple biological levels (e.g., individual, population, assemblage, and landscape) (Karr 1991, Karr and Chu 1999). Federal, state, and local agencies now apply these indexes to establish conservation priorities, determine the effects of land use practices, define restoration needs, evaluate the success of restoration activities, and guide regulatory actions throughout the United States (Davis and Simon

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1995, Davis et al. 1996, Cuffney et al. 1997, McCarron and Frydenborg 1997, Yoder and Rankin 1998, Barbour et al. 1999, Black and MacCoy 2000, Fore and Grafe 2002, U.S. Environmental Protection Agency 2002, Fore 2003).

Research in aquatic systems has demonstrated the utility of, and parallel conclusions from, studies of fish, benthic macroinvertebrates, and algae (Davis et al. 1996, Karr 1998, Fore 2003). Any major taxonomic group can be examined in an effective monitoring program; more important than which taxon is studied is the wisdom of the process of identifying and selecting metrics (Karr 1991).

The work reported here provides the first terrestrial analog of the aquatic IBI using the IBI development protocol, from study design and data collection to analysis and synthesis (Karr and Chu 1997, 1999, 2000). Key features of this approach include study of multiple study sites with varying histories of human influence, careful examination of data to identify biological measures (metrics) that provide reliable biological signal, and validation that patterns are consistent in multiple data sets (e.g., sample sites, regions, and years). Our studies of shrub-steppe landscapes included data collection at Department of Energy facilities in Washington (Hanford Nuclear Reservation) and in southeastern Idaho (Idaho National Engineering and Environmental Laboratory; INEEL). We sampled arthropods, vascular plants, and the macrobiotic soil crust; here we report only on our arthropod studies.

Arthropods are widely regarded as useful in monitoring and assessing biological systems (Moldenke and Lattin 1990, Kremen 1992, Didham et al. 1998). Although many assessments focus on one arthropod order or family as indicators of disturbance (Refseth 1980, Klein 1989, Neumann 1992, Niemala et al. 1993, Spitzer et al. 1997, Fabricius et al. 2003, Jones et al. 2003), the strength of multimetric indexes derives from the deliberate combination of diverse taxonomic, relative abundance, and ecological or functional measures into a single index. Using multiple metrics strengthens our ability to evaluate multiple dimensions of complex living systems. In addition, multimetric indexes dampen natural variability, or noise, at the metric level, because measures with high variance are excluded. When strong metrics are combined, the resulting terrestrial index of biological integrity (T-IBI), like IBIs for aquatic systems, provides a richer signal than, say, counts of endangered species: first, because it encompasses a number of biological contexts and, second, because it operates much like mathematical averages (Fore et al. 1994, Kimberling et al. 2001).

At Hanford we collected data for three years to identify metrics indicating the effects of human actions (Kimberling et al 2001). Our 25 Hanford study sites included undisturbed sites and disturbed sites (construction, dump, and agricultural). We identified attributes that were significantly correlated with history of human disturbance at our sites in two consecutive years (1997-98). (The probability that an attribute would have been chosen twice because of chance alone was $0.05^2$, or 0.0025.) Through this process we constructed a preliminary eight-metric Hanford T-IBI and validated those results with an independent data set from additional Hanford sites in a third year (1999) (Kimberling et al. 2001).

This paper describes the results of a similar study at INEEL and our effort to provide a more robust T-IBI that can be applied to the broader geographic area of northwest shrub-steppe. INEEL has both a large expanse of protected shrub-steppe and a recent history of diverse human activities. For example, approximately 40% of INEEL has been free from grazing for the past 45 yr (Anderson et al. 1996). The site was designated as a National Environmental Research Park in 1975 to protect its high ecological and biological value (Burger et al. 2003).

We sampled sites with various histories of human influence and posed the following questions: (1) How different are terrestrial arthropod assemblages at INEEL sites with different histories of human activity? (2) Can we select robust metrics and construct a multimetric index that is a reliable indicator of site condition? (3) Can the index be used to recognize biological differences among sites with different types of disturbance? (4) Are biological differences similar to those found at Hanford Nuclear Reservation in Washington State (Kimberling et al. 2001), where we applied the same methods, thereby allowing us to propose an index applicable to both regions?

## Methods

### Study Region and Sites

The 2300 $km^2$ INEEL features volcanic buttes, rhyolite domes, and unevenly surfaced basalt flows.

The region's relatively high elevation (average 1500 m) and its proximity to northern and western mountain ranges (Lost River, Lemhi, and Bitterroot) result in cold winters and hot, dry summers that constrain plant growth. Native vegetation consists of a shrub overstory and grass and forb understory. Sagebrush (*Artemesia* spp.) inhabits about 80% of the land; perennial grasses (*Poa* spp., *Agropyron* spp., *Festuca* spp., *Stipa* spp.) constitute the most abundant understory plants. Saltbush (*Atriplex* spp.) and winterfat (*Eurotia* spp.) are also widespread.

Cattle and sheep overgrazed most of the Intermountain West in the late 1800s (Wilkinson 1992, Belsky and Blumenthal 1997), but the extent to which grazing affected native plant communities at INEEL is unknown. Historical trails and roads indicate at least some grazing (Anderson et al. 1996). The construction of hundreds of kilometers of canals designed to carry water also influenced the region, although most canals were abandoned early in the 1900s. Before 1949 the military used the area as a testing range for naval guns from the U. S. Naval Ordnance Station in Pocatello, Idaho. Protected from public access for security reasons, the site was designated as a National Reactor Testing Station in 1949, renamed the Idaho National Engineering Laboratory in 1974, and given its present name in 1996.

We selected and sampled nine study sites in 1999 (Table 1, Figure 1) to match major environmental features (slope, soil type, elevation); all naturally supported shrub-steppe vegetation. Although we cannot know if all of our sites had equivalent natural biotas before human activity expanded in these regions in the past 200 yr, we match these natural attributes in an effort to minimize the probability of major differences in initial conditions among our sites. Our experimental design required sampling both minimally disturbed sites (natural areas) and sites with varying histories and types of human activities.

## Quantifying Disturbance

To select biological indicators, one must test and calibrate them against a gradient of human disturbance. Ecological principles and theory (e.g., from island biogeography, landscape ecology, and disturbance ecology) suggest that several key landscape features may serve as surrogates of human influence: area disturbed, frequency of disturbance, and time since last disturbance (Table 1). These measures seem both general and largely independent of type of human disturbance (physical, chemical, or biological). A fourth disturbance measure, extent of soil profile disruption, reflects the importance of soil disturbance and the role of the macrobiotic soil crust in regulating soil moisture, plant establishment, and plant and animal persistence in shrub-steppe environments (Belnap et al. 2001). For this study, we rated each criterion as high (2), medium-high (1.5), medium (1), medium-

TABLE 1. Principal human activity, and corresponding disturbance ratings, of the INEEL study sites shown in Figure 1. Disturbance ratings were based on areal extent of disturbance, soil profile disruption, time since disturbance, and frequency of disturbance. A site's overall rating equals the sum of its extent, soil, time, and frequency ratings.

| Site code[1] | Activity | Disturbance ratings[2] | | | | |
|---|---|---|---|---|---|---|
| | | Extent | Soil | Time | Frequency | Overall |
| UN-1 | Undisturbed | 0 | 0 | 0 | 0 | 0 |
| UN-2 | Undisturbed | 0 | 0 | 0 | 0 | 0 |
| CH-1 | Aerial chemical | 1.5 | 0 | 2 | 2 | 5.5 |
| RE-1 | Restoration | 1 | 2 | 2 | 1 | 6 |
| RE-2 | Restoration | 1 | 2 | 2 | 1 | 6 |
| GR-1 | Cattle grazing | 2 | 1 | 2 | 2 | 7 |
| GR-2 | Cattle grazing | 2 | 1 | 2 | 2 | 7 |
| PH-1 | Borrow pit | 1 | 2 | 2 | 1 | 6 |
| PH-2 | Gravel pit | 1.5 | 2 | 2 | 2 | 7.5 |

[1] First two letters of site code designate type of disturbance (UN = no known disturbance, CH = chemical disturbance, RE = physical disturbance followed by restoration, GR = cattle grazing, and PH = physical disturbance).

[2] Extent: 2 = > 200 ha, 1.5 = 21–199 ha, 1 = 6–20 ha, 0.5 = < 0.5 ha, 0 = undisturbed. Soil: 2 = deeply disturbed, 1 = minor surface disturbance, 0 = undisturbed. Time: 2 = < 10 yr, 1 = 10–20 yr, 0 = > 20 yr. Frequency: 2 = chronically disturbed, 1 = infrequently disturbed, 0 = undisturbed

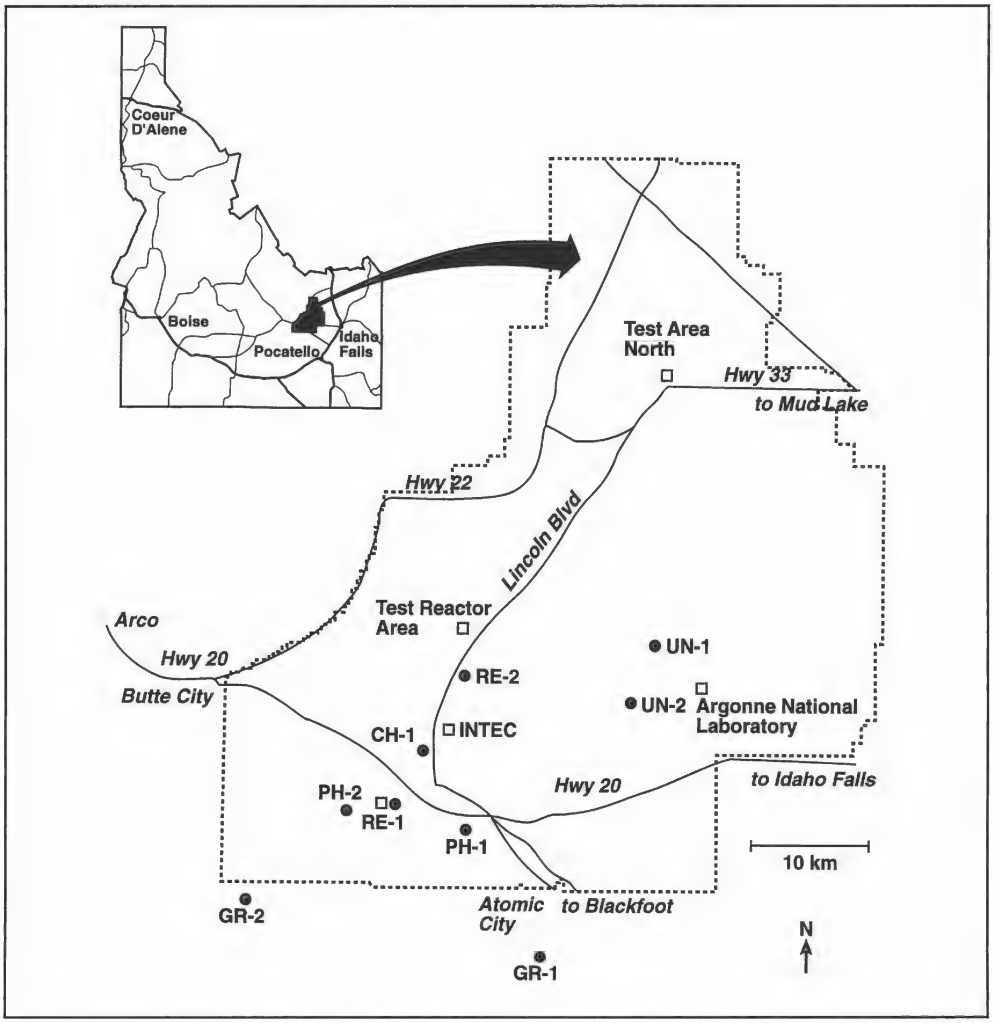


Figure 1. Idaho National Engineering and Environmental Laboratory study site locations (see Table 1 for human activities and degrees of disturbance at each site).

low (0.5), or low (0) to indicate the degree of each type of disturbance. The sum of scores for all disturbance classes is assumed to reflect relative disturbance levels at each site.

## Collecting Methods

We collected insects and other arthropods in simple pitfall traps (3 grids of 15 traps at each of 9 sites, see below). Each trap consisted of a 0.5 l plastic cup with a 0.2 l disposable cone cup—its bottom removed to create a funnel—inserted below the larger cup's lip. Each trap held a mixture of 50% water and 50% propylene glycol ~1.5 cm deep in the bottom. Traps were in place for seven nights and all sites were sampled within a 2-wk period (25 May to 7 June 1999). This period coincides with spring emergence and activity of herbaceous plants, grasses, and invertebrates but comes before the severe drought of summer, when many organisms become dormant.

We set three grids of 15 pitfall traps within each study site in three rows of five traps each at 5-m intervals; all study sites and the placement of grids within each site were defined to minimize border effects from surrounding areas with different disturbance histories. At Hanford, 15 traps per grid were sufficient to detect differences among sites reliably (Kimberling et al. 2001); the percentage of total variance due to measurement error (representing variability associated with replicate samples from the same site) declined from 58% with only one trap to 11% with 15 traps per replicate. Measurement error was similar at INEEL with 15 traps per replicate (Figure 2).

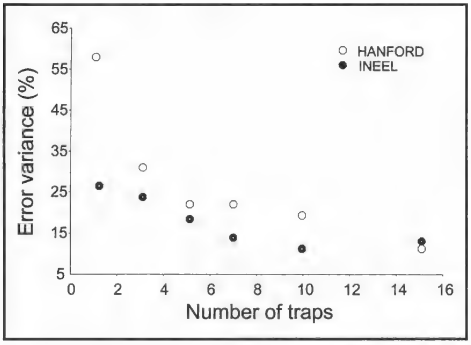


Figure 2. Error variance relative to sampling effort at Hanford (Kimberling et al. 2001) and INEEL. For overall species richness, the percentage of variance due to error declined as the number of traps per composite sample rose. The percentage error at INEEL (13%) came close to that at Hanford (11%) at 15 traps per sample.

Traps were collected at each site in the order they were set. We poured the contents of each trap onto a fine mesh screen (placed over a plastic jug for proper disposal); specimens remained on the screen. Samples were sealed into plastic bags with a 70% ethanol solution, and each grid of samples was put into a jar with 70% ethanol.

We sorted and identified the contents of each sample at the University of Washington in Seattle. Insects and spiders were sorted to order, family, genus (when possible), and species (when possible). Specimens that could not be identified to genus or species were assigned unique numbers as morphospecies. (For choosing metrics, either species or morphospecies would give equivalent taxa richness, or biodiversity.) We also evaluated attributes that applied to broader taxonomic categories than species (e.g., family: all Tachinidae are parasitic flies). We consulted taxonomic experts for further identification within orders and to confirm morphospecies.

### Data Analysis

First, we developed a list of 56 attributes of arthropod assemblages for evaluation. These were tested for significant differences (Spearman's $r$, $P < 0.05$) along a gradient of human disturbance, a winnowing process that yielded 21 attributes for further evaluation. Second, we selected the best eight for inclusion in a multimetric IBI (T-IBI) by removing those that were biological redundant, behaved erratically relative to our hypotheses, or were not significant at $P < 0.01$. Finally, we calculated a T-IBI for each study site and tested the T-IBI values for their correlation with disturbance using Spearman's $r$.

Whenever an IBI is developed, disparate quantitative scales of the original attributes require converting the attributes' units of measure to a common scoring base (Karr et al. 1986, Kerans and Karr 1994, Fore et al. 1996). We assigned scores of 5, 3, or 1 to each of the metrics with clear dose-response curves, where 5 represented the quantitative values found at minimally disturbed sites (natural or reference condition), 3 represented moderate deviation from reference condition, and 1 represented a strong deviation from reference condition. We assigned the range of metric values associated with undisturbed sites a score of 5 and divided half the range of metric values for disturbed sites and assigned a score of 3 or 1 to each half (Kimberling et al. 2001). Metric scores (5, 3, or 1) were then summed to yield a site T-IBI.

## Results

### Quantifying Disturbance

Measured by our four disturbance criteria—area of disturbance, soil profile disruption, time since disturbance, and disturbance frequency—disturbance ratings ranged from 0 to 7.5 (Table 1). Sites with rating 0 were the least disturbed (UN-1, UN-2), and sites scoring 7 or more were most disturbed (GR-1, GR-2, PH-2).

### Field Samples

Our sample of 405 pitfall traps across the 9 study sites contained 23,165 insects (excluding

Collembola), spiders, and other arthropods representing 19 orders, 140 families, and 531 species. The number of specimens per grid varied widely among the sites, although within a site, sample size varied much less. Undisturbed sites UN-1 and UN-2 averaged 2171 and 773 specimens per grid, whereas the most disturbed site, PH-2, averaged 100 specimens per grid. We captured the fewest arthropods at PH-2, the relatively barren gravel pit often disrupted by heavy equipment. Large numbers of ants (69% of captured individuals) increased sample sizes at UN-1.

## Biological Attributes and Human Disturbance

Of the 56 attributes tested, 21 showed significant differences along a gradient of disturbance ($P < 0.05$) (Table 2). For three attributes (relative abundance of the harvester ant *Pogonomyrmex,* relative abundance of parasitoids, and relative abundance of parasitic Hymenoptera), quantitative changes along the gradient, although significant, contradicted our predictions; we predicted that the relative abundance of the ant *Pogonomyrmex* would increase and the relative abundance of parasitoids and parasitic Hymenoptera would decrease along our disturbance gradient. Those attributes were not considered further.

Eight attributes were significant at $P < 0.05$ and 10 at $P < 0.01$. Because our data were limited to only one year, we used a high standard of association and focused on the 10 attributes with $P < 0.01$. Two pairs of biologically redundant measures were included among the 10 (total species

TABLE 2. Predicted responses of attributes of the arthropod assemblage at INEEL sites, and the statistical correlation of these attributes to human disturbance. A *T* preceding a name indicates taxa richness of that group; a *P*, its relative abundance expressed as a percentage of total individual organisms. Correlation was determined by Spearman's *r*; X indicates that the actual response was the opposite of the predicted response. INEEL T-IBI metrics appear in bold.

| Attribute | Predicted response | Spearman's *r* ($n = 9$) | Attribute | Predicted response | Spearman's *r* ($n = 9$) |
|---|---|---|---|---|---|
| Tspecies | Decrease | $P < 0.01$ | PCollembola | Increase | |
| **Tfamily** | Decrease | $P < 0.01$ | **TAcarina** | Decrease | $P < 0.01$ |
| TColeoptera | Decrease | $P < 0.05$ | PAcarina | Decrease | $P < 0.01$ |
| PColeoptera | Decrease | | TLepidoptera | Decrease | |
| TCarabidae | Decrease | | THemiptera | Decrease | $P < 0.05$ |
| PCarabidae | Increase | | PHemiptera | Increase | |
| Tpolyphagous Carabidae | Increase | | Tparasitoids | Decrease | |
| Ppolyphagous Carabidae | Increase | | Pparasitoids | Decrease | X |
| TElateridae | Decrease | | Tparasitic Hymenoptera | Decrease | |
| PElateridae | Decrease | | Pparasitic Hymenoptera | Decrease | X |
| **TTenebrionidae** | Decrease | $P < 0.01$ | **Tdetritivores** | Decrease | $P < 0.01$ |
| PTenebrionidae | Decrease | | Pdetritivores | Decrease | |
| TEleodes | Decrease | $P < 0.05$ | Pdetritivores (minus Collembola) | Decrease | |
| PEleodes | Decrease | | **Tpredators** | Decrease | $P < 0.01$ |
| TAraneae | Decrease | $P < 0.05$ | Ppredators | Increase | |
| PAraneae | Increase | | Therbivores | Decrease | $P < 0.05$ |
| Tweb/Araneae | Decrease | | Pherbivores | Increase | |
| Tweb/Araneae | Decrease | | Tpollinators | Decrease | |
| Tno web/Araneae | Decrease | $P < 0.05$ | Ppollinators | Increase | |
| Pno web/Araneae | Increase | | **Tground** | Decrease | $P < 0.01$ |
| THomoptera | Decrease | $P < 0.05$ | Pground | Decrease | |
| PHomoptera | Increase | | Pdominance (3 families) | Increase | |
| **TDiptera families** | Decrease | $P < 0.01$ | Pdominance (minus Collembola) | Increase | |
| TTachinidae | Decrease | | Pdominance (minus Formicidae) | Increase | $P < 0.05$ |
| PTachinidae | Decrease | | Trare | Decrease | |
| **THymenoptera** | Decrease | $P < 0.01$ | No. individuals (minus Collembola) | Increase | |
| PHymenoptera | Increase | | | | |
| TFormicidae | Decrease | | | | |
| PFormicidae | Increase | | | | |
| P*Pogonomyrmex* | Increase | X | | | |

TABLE 3. Metric and index values for all INEEL sites (average of three samples per site; see Table 1 for site descriptions). Metrics beginning with a T measure taxa richness. Numbers in parentheses represent metric scores (5, reference or undisturbed conditions; 3, moderate deviation from reference; 1, strong deviation from reference), assigned on the basis of research at Hanford (Kimberling et al. 2001). Minimum T-IBI value equals 8, maximum equals 40.

| Site code | Metrics[1] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Tfamily | TTenebrionidae | TDiptera | THymenoptera | TAcarina | Tpredators | Tdetritivores | Tground | T-IBI |
| UN-1 | 67 (5) | 4.3 (3) | 14.7 (3) | 22.3 (5) | 6.3 (5) | 28.7 (5) | 17.7 (5) | 37.3 (5) | 36 |
| UN-2 | 63 (5) | 5.7 (5) | 13.7 (3) | 25.3 (5) | 6.3 (5) | 28 (5) | 16.3 (5) | 36.3 (5) | 38 |
| CH-1 | 55.3 (5) | 3.7 (3) | 12.3 (3) | 21.0 (3) | 5.7 (5) | 17.7 (3) | 12 (3) | 29.7 (3) | 28 |
| RE-1 | 55.3 (5) | 2.7 (1) | 13.7 (3) | 21.7 (3) | 1.3 (3) | 22.7 (3) | 14 (5) | 33.7 (5) | 28 |
| RE-2 | 54.3 (5) | 3.3 (3) | 12.3 (3) | 22.7 (5) | 0.3 (1) | 21 (3) | 16.3 (5) | 31.7 (5) | 30 |
| GR-1 | 49 (5) | 2.7 (1) | 10.3 (1) | 22.0 (3) | 3 (5) | 14.7 (1) | 12 (3) | 27 (3) | 22 |
| GR-2 | 48 (5) | 2.7 (1) | 12 (3) | 14.3 (1) | 1.7 (3) | 15.3 ( 3) | 11.7 (3) | 26.3 (3) | 22 |
| PH-1 | 43.3 (3) | 1.7 (1) | 9.7 (1) | 17.0 (3) | 2.3 (5) | 14.3 (1) | 9.3 (1) | 25.7 (3) | 18 |
| PH-2 | 26.7 (1) | 0.7 (1) | 5.3 (1) | 9.0 (1) | 0 (1) | 8.3 (1) | 4.7 (1) | 7.7 (1) | 8 |

[1]Metrics: Tfamily = overall family richness; TTenebrionidae = Tenebrionid species richness; TDiptera = Diptera family richness; THymenoptera = bees, wasps, and allies species richness; TAcarina = Acarina species richness, Tpredators = predator species richness, Tdetritivores = detritivore species richness, and Tground = ground-dwelling species richness.

richness and total family richness; taxa richness of mites and relative abundance of mites). We therefore dropped one measure from each pair, total species richness and relative abundance of mites, from further consideration. Eight attributes with significant ($P < 0.01$) dose-response curves remained (Table 3): total family taxa richness; fly (Diptera) family richness; species richness of darkling beetles (Tenebrionidae), mites, detritivores, predators, adult ground dwellers, and bees, wasps, and allies (Hymenoptera).

We chose those eight metrics to define a T-IBI specific to our INEEL data set that is significantly correlated ($P = 0.011$) with disturbance rating (Figure 3). The INEEL T-IBI yields site assessments that range from 36 and 38 (Table 3) for the two undisturbed sites (maximum = 40) to 8 and 18 for physically disturbed sites (minimum = 8).

Many dimensions of INEEL's biota—individual attributes and the resulting index—varied among our study sites. Physical disturbance (PH-2) was most devastating to biological condition: family richness at physically disturbed sites differed by 60% from that at undisturbed sites (UN-1, UN-2); richness of fly families by 64%; species richness of ground beetles by 85%, predators by 70%, and detritivores by 73%. Continual operation of heavy equipment in the gravel pit (PH-2), for example, where the soil was compacted, apparently prevented most organisms from establishing resident populations there. Limited recent activity at the borrow pit (PH-1) permitted some

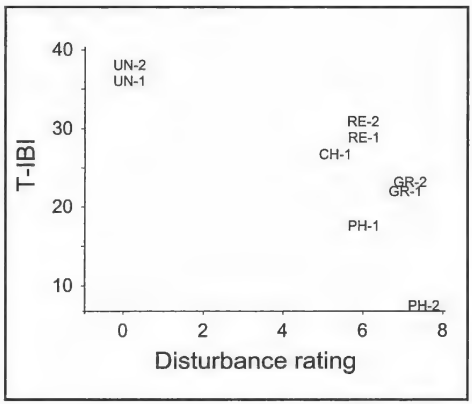


Figure 3. Relationship between disturbance rating at nine INEEL shrub-steppe sites and T-IBI (Spearman's $r = -0.814$).

reestablishment of vegetation and a more diverse arthropod fauna. Sites with some restoration had improved biological condition compared with physically disturbed but unrestored sites. Grazed (22, 22), restored (28, 30) and chemically contaminated (28) sites had intermediate T-IBIs. Severe soil compaction, either from the hooves of livestock or from past construction, influenced these sites.

## Discussion

Our research at INEEL demonstrates that we can formulate a measure of human activity reflecting multiple human influences. Moreover, our

exploration of the differences in terrestrial arthropods at sites with different histories of human influence shows that eight biological measures correlate significantly with degree of human disturbance. Those eight measures can be combined to produce a multimetric biological index (T-IBI)—an integrative evaluation of the biological effects of varying histories of human activities at each of the nine INEEL study sites.

T-IBI captures the often extreme biological changes that have occurred, changes that are not normally reflected by more narrow measures such as counts of threatened and endangered species. The level of significance for the correlations between metrics and disturbance rating ($P < 0.01$), combined with divergent index values for sites with different disturbance histories, reinforces our confidence in this approach to biological assessment.

Still, our limited data set (nine sites and one year) make it inappropriate to overinterpret (or extrapolate) our results, even if we can find detailed, statistically significant patterns in the data. Very detailed statistical analyses of small data sets lack credibility in validating a measurement tool for broad applicability. We therefore compared our INEEL results with a larger data set from the Hanford Nuclear Reservation in Washington State (Kimberling et al. 2001).

The Hanford T-IBI was strongly associated with human disturbance in all 3 yr (Kimberling et al. 2001). Index values varied widely, depending on land-use history and current human activity. We found, for example, that the Arid Lands Ecology (ALE) Reserve had a T-IBI of 34 (maximum 40), but the old Hanford town site, abandoned in the 1940s, had a T-IBI of only 10 (minimum 8). Differences in specific metrics from minimally disturbed sites to severely altered areas included species richness, or biodiversity, that was lower in ground dwellers (23%), predators (34%), detritivores (51%), and mites (87%). Family richness was lower by 40%. Our Hanford T-IBI captured variation in arthropods associated with our study sites' different histories of human influence.

Although the terrestrial arthropod faunas at INEEL and Hanford are not identical, they are similar; 35% (187) of the 531 species found at INEEL also occurred in our Hanford samples. We evaluated 56 biological measures from one year of INEEL data; 21 (38%) showed significant dose-response relationships to human influence, a number that is strikingly similar to the 19 (33%) and 22 (39%) of 57 significant attributes in the Hanford data for 1997 and 1998 (Kimberling et al 2001). We used these similarities to develop a generally applicable shrub-steppe T-IBI, in much the same way as a benthic invertebrate IBI (B-IBI) was developed for streams in Tennessee, the Pacific Northwest, and Japan (Karr 1998).

A total of 12 biological attributes met our standards of association between disturbance rating and biological condition at Hanford (8 metrics out of the 12, 2 yr, $P < 0.05$) and INEEL (10 metrics out of 12, 1 yr, $P < 0.01$) (Table 4). Six metrics with clear dose-response relationships to disturbance—total family richness; Diptera family richness; Acarina species richness; predator species richness; detritivore species richness; and adult ground dweller species richness—overlapped at Hanford and INEEL. In other words, the same dominant biological characters changed in response to diverse human influences at shrub-steppe sites of Washington and Idaho. Thus it is reasonable to include at least those core 6 metrics in a preliminary shrub-steppe T-IBI. Indeed, a T-IBI composed of those six metrics correlated very strongly with the disturbance gradient for our nine INEEL sites ($P < 0.001$) (Table 5).

Two metrics in the Hanford index—polyphagous Carabid species richness and relative abundance of Collembola—did not correlate significantly with disturbance rating at INEEL. Conversely, two metrics in the Idaho index—species richness of darkling beetles (Tenebrionidae) and species richness of bees, wasps, and allies (Hymenoptera)—did not go into the Hanford index. When the two Hanford metrics are added to the overlapping core six metrics—the Hanford T-IBI (WA 8)—the resulting index correlates with disturbance at INEEL to the same extent as the original INEEL T-IBI (ID-8, $P = 0.011$; WA-8; $P = 0.004$) (Table 5, Figure 4). In effect, the correlation between the disturbance gradient and biological condition at INEEL is significant whether measured by metrics defined by analysis of Hanford or INEEL data.

Combining analyses at both INEEL and Hanford yields nine metrics correlated significantly with disturbance rating in three out of four years, regardless of study region (Best 9, $P < 0.002$) (Table 5). These 9 constitute the most inclusive list of metrics; biological condition as measured by those 9 metrics is correlated with human disturbance rating at INEEL (Figure 4). We conclude that a

TABLE 4. Twelve metrics meeting our criteria (see text) for inclusion in an arthropod T-IBI at shrub-steppe study sites in Washington (data from 1997, 1998, and 1999) and Idaho (data from 1999 only), their level of significance ($P$) when statistically tested against a human disturbance gradient, and the metrics included in each of four alternative T-IBIs. A yes indicates that the metric was used to construct the given T-IBI. We recommend combining the best nine metrics from both Washington and Idaho to produce the most integrative and generally applicable index for shrub-steppe. See Table 2 for all metrics evaluated.

| Metric[1] | Idaho 1999[2] | ID 8 T-IBI[3] | Washington 1997[4] | Washington 1998[4] | Washington 1999[2] | WA 8[5] T-IBI | Core 6[6] T-IBI | Best 9[7] T-IBI |
|---|---|---|---|---|---|---|---|---|
| Tspecies | 0.01 | | — | 0.05 | — | | | |
| Tfamilies | 0.01 | Yes | 0.055 | 0.01 | 0.01 | Yes | Yes | Yes |
| Tpolyphagous Carabidae | — | | 0.055 | 0.01 | 0.01 | Yes | | Yes |
| TTenebrionidae | 0.01 | Yes | 0.01 | — | 0.01 | | | Yes |
| TDiptera families | 0.01 | Yes | 0.055 | 0.01 | 0.058 | Yes | Yes | Yes |
| THymenoptera | 0.01 | Yes | — | — | — | | | |
| PCollembola | — | | 0.055 | 0.05 | 0.05 | Yes | | Yes |
| TAcarina | 0.01 | Yes | 0.01 | 0.05 | 0.058 | Yes | Yes | Yes |
| PAcarina | 0.01 | | 0.055 | — | 0.01 | | | |
| Tdetritivores | 0.01 | Yes | 0.01 | 0.05 | 0.01 | Yes | Yes | Yes |
| Tpredators | 0.01 | Yes | 0.055 | 0.01 | 0.01 | Yes | Yes | Yes |
| Tground-dwelling adults | 0.01 | Yes | 0.055 | 0.05 | 0.05 | Yes | Yes | Yes |

[1] T as a metric prefix indicates a taxa richness measure; P indicates relative abundance.
[2] Numbers represent $P <$ for Spearman's $r$.
[3] Idaho 8: eight metrics selected for a T-IBI on the basis of INEEL data.
[4] $P <$ indicated value for Mann-Whitney U-test.
[5] Washington 8: eight metrics selected for a T-IBI on the basis of Hanford data.
[6] Six metrics that appear in both ID 8 and WA 8 T-IBIs.
[7] Nine metrics highly correlated with human disturbance in three out of four years' data from either Hanford or INEEL. The T-IBI built of these metrics would be most generally applicable.

TABLE 5. Overall disturbance ratings for our nine INEEL study sites and T-IBIs for those sites using four alternative combinations of metrics (see Table 4 for metrics included in each T-IBI). ID 8: T-IBI based on eight metrics from INEEL data. WA 8: T-IBI based on eight metrics from Hanford data. Core 6: T-IBI based on six metrics in both ID 8 and WA 8. Best 9: T-IBI based on the best nine metrics from both INEEL and Hanford data and most generally applicable to shrub-steppe.

| Site code | Disturbance rating | T-IBI ID 8 | T-IBI WA 8 | T-IBI Core 6 | T-IBI Best 9 |
|---|---|---|---|---|---|
| UN-1 | 0 | 36 | 38 | 28 | 41 |
| UN-2 | 0 | 38 | 36 | 28 | 41 |
| CH-2 | 5.5 | 28 | 32 | 22 | 35 |
| RE-1 | 6 | 28 | 26 | 24 | 27 |
| RE-2 | 6 | 30 | 28 | 22 | 31 |
| GR-1 | 7 | 22 | 26 | 18 | 27 |
| GR-2 | 7 | 22 | 28 | 20 | 28 |
| PH-1 | 6 | 18 | 22 | 14 | 22 |
| PH-2 | 7.5 | 8 | 16 | 6 | 16 |
| Spearman's $r$ | | –0.814 | –0.810 | –0.845 | –0.832 |
| $P$ | | 0.011 | 0.004 | <0.001 | 0.002 |

generally applicable shrub-steppe T-IBI can be constructed from the sum of our work in two separate shrub-steppe regions. We recommend using nine metrics in a shrub-steppe T-IBI to maximize the number of rigorously defined biological dimensions going into an assessment of shrub-steppe condition.

As noted in Methods, we used a scoring system (5, 3, or 1) to convert raw measurements of biological attributes to a common base, so that metrics based on different units can be added together in a single index. We developed scoring boundaries for our shrub-steppe T-IBI on the basis of Hanford research. We recognize that some metrics may have broader ranges in other study regions. For example, family richness at undisturbed Hanford sites (range, 48–61 families) was generally lower than at undisturbed INEEL sites (range, 63–67 families). When we applied the same thresholds used at Hanford to our INEEL data, most INEEL sites scored a 5, because INEEL's taxa richness was generally higher at all sites. For

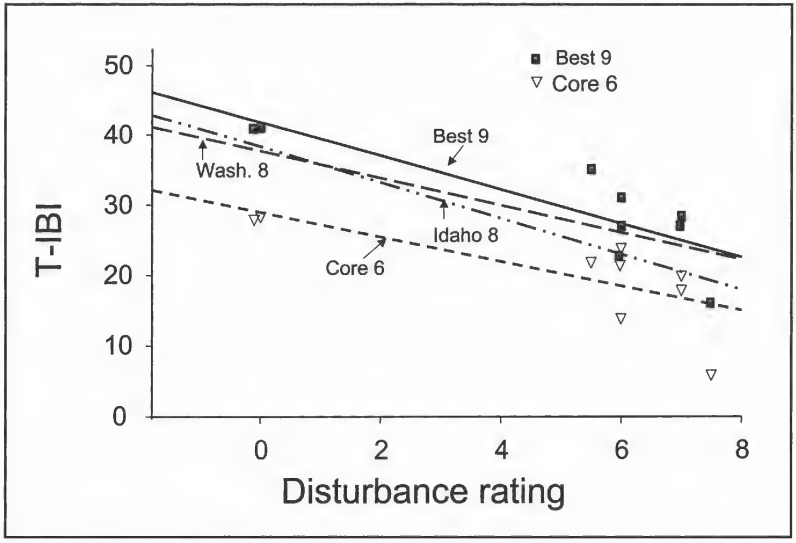


Figure 4. Relationship between disturbance rating at nine INEEL sites and T-IBIs based on four alternative combinations of metrics. Data and regression line shown for Core 6 and Best 9 T-IBIs; regression line only for ID 8 and WA 8 T-IBIs. See Tables 4 and 5 for description of alternative combinations of metrics.

this metric, then, adjusting the boundary levels needed to score a 5 (e.g., from 47 to 60) would likely provide a more accurate assessment of sites at INEEL.

We do not know whether the differences in taxa richness between the two areas reflect differences in the biota (higher natural biodiversity at INEEL) or differences in the history of human influence (more human-caused degradation at Hanford). It will take more study to resolve such scoring-threshold questions. For present purposes, we did not adjust scoring thresholds. The result is that the absolute values of T-IBI for the best Hanford sites fall below those for the best INEEL sites. Without further research we cannot know if the discrepancy reflects real discrepancies in biological condition (histories of human influence) or imprecise scoring because we do not recognize real differences in biological diversity in our two study regions.

## Observations

We offer other observations that may help with interpretation of future monitoring and assessment studies. First, the only two metrics that increased significantly with increasing human influence at Hanford—the percentage relative abundance of Collembola and polyphagous carabid taxa richness—were not significant at INEEL. None of the metrics in our recommended nine-metric T-IBI increased with human influence. When faced with severe or incessant disturbance (for example, like that in the gravel pit at INEEL, where little survives), even those groups favored by disturbance may not be able to persist, a situation also encountered in aquatic systems and for which appropriate scoring adjustments are available (Rankin and Yoder 1999).

Second, when choosing metrics for a multimetric index, one should avoid those that are biologically redundant (Karr and Chu 1999). Our decision to exclude two significant INEEL metrics (species richness and mite relative abundance, which were redundant with family richness and mite richness) from the final nine-metric T-IBI did just that. Nevertheless, three of the nine T-IBI metrics were more redundant biologically at INEEL than at Hanford. Nearly two-thirds of detritivore species were also adult ground dwellers, and more than one-third of predator taxa were also ground dwellers. Ground-dwelling taxa are

likely sensitive to soil and understory disruptions that interfere with their life cycles; detritivores may also be more susceptible than other taxa to changes in the soil or litter composition because of their often sedentary nature (Moldenke and Lattin 1990). Predators may be more affected by disturbance as their prey populations decline or become fragmented (Didham et al. 1998). Although excessive biological redundancy among metrics may justify eliminating metrics in some circumstances, we believe that the overlap among our nine metrics is not large enough to outweigh the increased resolution that comes from including more highly significant metrics in the index.

Our combined Hanford and INEEL studies show that T-IBI metrics are sensitive to human influences over more than one isolated geographic area. Our results reinforce the view that the principles embodied in multimetric indexes meet the National Research Council's criteria for good ecological indicators: they reflect diverse dimensions of the system under study, simplify information about complex phenomena to improve communication with interested parties, and are cost-effective (National Academy of Sciences 2000). Measures of biological condition, such as T-IBI, incorporate a depth and breadth that goes beyond counts of threatened, endangered, or commodity species. They also highlight the important links among taxa, composition, and function in ecological systems—the parts and processes that constitute a living system's integrity.

Ecological, especially biological, indicators are central to any effort to measure and understand the environmental consequences of human actions. Because biological indicators track the status of, and trends in, living systems, they provide the single most relevant means of evaluating the effectiveness of conservation, cleanup, remediation, and restoration. They also serve as the most appropriate report card of compliance with federal and state laws, such as the Clean Water Act or state and local growth management acts. Such indicators can and should guide policy and direct research (National Academy of Sciences 2000).

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## Literature Cited

Anderson, J. E., K. T. Ruppel, J. M. Glennon, K. E. Holte, and R. C. Rope. 1996. Plant communities, ethnoecology, and flora of the Idaho National Engineering Laboratory. Environmental Science and Research Foundation Report Series, Number 005, ESRF, Idaho Falls, Idaho.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: Periphyton, benthic macroinvertebrates and fish, second edition. Publication EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, D.C.

Belnap, J., R. Rosentreter, S. Leonard, J. H. Kaltenecker, J. Williams, and D. Eldridge. 2001. Biological Soil Crusts: Ecology and Management. Publication Technical Reference 1730-2. United States Department of Interior, Bureau of Land Management, United States Geological Survey Forest and Rangeland Ecosystem Science Center, National Science and Technology Center, Denver, Colorado.

Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology 11:315-327.

Black, R. W., and D. E. MacCoy. 2000. The development and evaluation of a benthic index of biological integrity for the Cedar River Watershed, Washington. Water Resources Investigations Report 99-4203. U.S. Geological Survey, Tacoma, Washington.

Burger, J., T. M. Leschine, M. Greenberg, J. R. Karr, M. Gochfeld, and C. W. Powers. 2003. Shifting priorities at the Department of Energy's bomb factories: Protecting human and ecological health. Environmental Management 31:157-167.

Cuffney, T. F., M. R. Meador, S. D. Porter, and M. E. Gurtz. 1997. Distribution of fish, benthic invertebrate, and algal communities in relation to physical and chemical

conditions, Yakima River Basin, Washington, 1990. Water-Resources Investigations Report 96-4280. U.S. Geological Survey, Raleigh, North Carolina.

Davis, W. S. 1999. Foreword. Pages iii-iv *In* T. P. Simon (editor). Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities. CRC Press, Boca Raton, Florida.

Davis, W. S., and T. P. Simon (editors). 1995. Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. Lewis Publishers, Boca Raton, Florida.

Davis, W. S., B. C. Snyder, J. B. Stribling, and C. Stoughton. 1996. Summary of state biological assessment programs for streams and rivers. Publication EPA 230-R-96-007. Environmental Protection Agency, Office of Policy, Planning, and Evaluation, Washington, D.C.

Didham, R. K., J. H. Lawton, P. M. Hammond, and P. Eggleton. 1998. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philosophical Transactions of the Royal Society of London. Series B 353:437-451.

Fabricius, C., M. Burger, and P. A. R. Hockey. 2003. Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thichet, South Africa: arthropods and reptiles. Journal of Applied Ecology 40:392-403.

Fore, L S. 2003. Responses of diatom assemblages to human disturbance: Development and testing of a multimetric index for the Mid-Atlantic region (USA). Pages 445-480 *In* T. P. Simon, editor. Biological Response Signatures: Indicator Patterns Using Aquatic Communities. CRC Press, Boca Raton, Florida.

Fore, L. S., and C. Grafe. 2002. Using diatoms to assess the biological condition of large rivers in Idaho (USA). Freshwater Biology 47:2015-2037.

Fore, L. S., J. R. Karr, and L. L. Conquest. 1994. Statistical properties of an index of biological integrity used to evaluate water resources. Canadian Journal of Fisheries and Aquatic Sciences 51:1077-1087.

Fore, L. S., J. R. Karr, and R. W. Wisseman. 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. Journal of the North American Benthological Society 15:212-231.

Jones, D. T., F. X. Susilo, D. E. Bignell, S. Hardiwinoto, A. N. Gillison, and P. Eggleton. 2003. Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. Journal of Applied Ecology 40:380-391.

Karr, J. R. 1991. Biological integrity: A long-neglected aspect of water resource management. Ecological Applications 1:66-84.

Karr, J. R. 1998. Rivers as sentinels: Using the biology of rivers to guide landscape management. Pages 502-528 *In* R. J. Naiman and R. E. Bilby (editors). River Ecology and Management: Lessons from the Pacific Coastal Ecosystems. Springer, New York.

Karr, J. R., K. D. Fausch, P. L. Angermeier, P. R. Yant, and I. J. Schlosser. 1986. Assessing biological integrity in running waters: A method and its rationale. Special Publication 5, Illinois Natural History Survey, Urbana, Illinois.

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Karr, J. R., and E. W. Chu. 1997. Biological monitoring: Essential foundation for ecological risk assessment. Human and Ecological Risk Assessment 3:993-1004.

Karr, J. R., and E. W. Chu. 1999. Restoring Life in Running Waters: Better Biological Monitoring. Island Press, Washington, D.C.

Karr, J. R., and E. W. Chu. 2000. Sustaining living rivers. Hydrobiologia 422/423:1-14.

Kerans, B. L., and J. R. Karr. 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. Ecological Applications 4:768-785.

Kimberling, D. N., J. R. Karr, and L. S. Fore. 2001. Measuring human disturbance using terrestrial invertebrates in the shrub-steppe of eastern Washington (USA). Ecological Indicators 1:63-81.

Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology 70:1715-1725.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications 2:203-217.

McCarron, E., and R. Frydenborg. 1997. The Florida bioassessment program: An agent for change. Human and Ecological Risk Assessment 3:967-977.

Moldenke, A. R., and J. D. Lattin. 1990. Dispersal characteristics of old-growth soil arthropods: The potential for loss of diversity and biological function. Northwest Environmental Journal 6:408-409.

National Academy of Sciences. 2000. Ecological Indicators for the Nation. National Academy Press, Washington, D.C.

Neumann, F. G. 1992. Responses of foraging ant populations to high intensity wildfire, salvage logging, and natural regeneration processes in *Eucalyptus regnans* regrowth forest of the Victorian central highlands. Australian Forestry 55:29-38.

Niemela, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology 7:551-561.

Rankin, E. T., and C. O. Yoder. 1999. Methods for deriving maximum species richness lines and other threshold relationships in biological field data. Pages 611-624 *In* T. P. Simon (editor). Assessing the Sustainability and Biological Integrity of Water Resources Using Fish Communities. CRC Press, Boca Raton, Florida.

Refseth, D. 1980. Ecological analyses of carabid communities: Potential use in biological classification for nature conservation. Biological Conservation 17:131-141.

Spitzer, K., J. Jaros, J. Havelka, and J. Leps. 1997. Effects of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. Biological Conservation 80:9-15.

U.S. Environmental Protection Agency. 2002. Summary of biological assessment programs and biocriteria development for states, tribes, territories, and interstate commissions: streams and wadeable rivers. EPA-822-R-02-048. U.S. Environmental Protection Agency, Washington, DC.

Wilkinson, C. F. 1992. Crossing the Next Meridian: Land, Water, and the Future of the West. Island Press, Washington, D.C.

Yoder, C. O., and E. T. Rankin. 1998. The role of biological indicators in a state water quality management process. Environmental Monitoring and Assessment 51:61-88.

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# Home Range Use of Coyotes: Revisited

## Abstract

The sagebrush-steppe is a seemingly homogeneous community in southeastern Idaho, nevertheless coyotes in this community do not use their home ranges uniformly. Also, they display two different movements: back-and-forth (B) and ranging (C). We used a GIS analysis to test if coyotes were selecting specific habitat characteristics in this community and if there was a relationship between habitats selected and B and C type movements. Our results show that coyotes exhibit habitat selection within their home range with sagebrush on and off lava as the preferred habitats. They also selected primarily sagebrush-steppe on lava habitat for B movements and sagebrush off lava habitat for C movements. During their 24 hr travels, males and females used different habitat combinations for both B and C movements. Males primarily used the sagebrush on and off lava habitats while females commonly used a wider range of habitat types. There were significant differences in habitat composition of areas coyotes used daily relative to season. Coyotes in general used a greater diversity of habitat types during the pair formation and pup rearing but concentrated their activity in the sagebrush-steppe on lava habitat during gestation. We suggest that coyotes used differing behaviors in different habitat types to meet their daily/seasonal food needs.

## Introduction

Coyotes are medium sized canids that occupy a variety of habitats in much of North America. Because of their ubiquitous distribution and frequent conflicts with human activities, there have been numerous studies of their ecology and behavior. Various investigators have studied habitat selection and have amply demonstrated that coyotes prefer certain habitat types and actively avoid others (Ozoga and Harger 1966, Gipson and Sealander 1972, Berg and Chesness 1978, Andelt and Gipson 1979, Litvaitis and Shaw 1980, Roy and Dorrance 1985, Gese et al. 1988, Holzman et al. 1992, Hernández et al. 1993, Murry et al. 1994). Additionally, some have reported differences in habitat use among seasons (Person and Hirth 1991).

In addition to demonstrating habitat selection by coyotes, some investigators have implied coyotes will select habitats for different behaviors such as for resting (Andelt and Gipson 1979) or for hunting (Chesness and Bremicker 1974, Murry et al. 1994, Oehler and Litvaitis 1995). Others have even shown that hunting success varies among habitat types (Murry et al. 1994, Gese et al. 1995), providing a possible rational for preferred use. However, the main objective of these studies was not to test the hypothesis that coyotes were selecting different habitats for different behaviors.

Coyotes in southeastern Idaho use two distinct movement types within the 24-hr cycle (Laundré and Keller 1981). Type B movements are characterized by relatively small distances (<0. 25 km) between relocations and produced a back and forth or zig zag pattern. Type C movements were characterized by longer distances between relocations which produced a much more elongated pattern. They also found home ranges consisted of areas of high and low use reflecting different combinations of frequency of use of these movement types. Additionally, coyotes use different proportions of types B and C movements between the sexes and through the year. Laundré and Keller (1981) proposed that these two movement types possibly represented different hunting strategies and that dissimilarities in their use represented differences/changes in the needs of males and females over the reproductive cycle, for instance, more territorial activity by males during pair formation (Camenzind 1978). Finally, they hypothesized that the differing spatial and temporal occurrence of the two behaviors corresponded to selection of habitat based on vegetational and structural differences in areas used for each strategy.

Laundré and Wilkosz (1991) attempted to test the hypothesis that areas used for different behaviors by coyotes were related to habitat composition by measuring various habitat characteristics of areas used by coyotes. They measured percent cover of each perennial plant species, litter, rock, bare ground, and dead sagebrush and

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found a weak association between types of behaviors and some habitat characteristics. However, the sample consisted of only four animals (two males and two females). They concluded a larger sample size would be necessary to test the hypothesis that coyotes selected certain habitat types for specific behaviors within the sage-steppe environment.

With the advent of Geographical Information System (GIS) capabilities, such a larger scale analysis is now possible. A detailed (30 m x 30 m pixels) GIS habitat map based on satellite images from 1987 and 1989 (Anderson et al. 1996) is now available for the area. Dominant community structure (shrubs-grasslands) does not change significantly over time (Anderson and Holte 1981). Thus, the overall habitat structure of the area would not have changed significantly in the 10 yr between collection of the telemetry data (1977-78) and the construction of the habitat map. Consequently, we have the opportunity to use this map with the original telemetry locations of coyotes, to test the hypothesis that different movements, and thus patterns of habitat use by coyotes, are related to different habitats.

We tested five predictions: 1) habitat characteristics of the home range area (the area coyotes select to live) will differ from the overall surrounding area (within 300 m around and including the home range area); 2) within the home range, areas of type B movement differ in habitat type compared to areas of type C movement; 3) the habitat types coyotes use for types B and C movements during their 24-hr travels differ; 4) the sexes use habitat differently for the two movement types; and 5) because coyotes exhibit a seasonal difference in the type of movements they use, there will be seasonal difference in overall daily habitat use.

To test these predictions and the hypothesis that coyotes are selecting different habitat types for different types of movements, we conducted a GIS analysis of habitat types relative to the different use types defined above. Results of our analysis should help determine if coyotes are selecting habitats based on their potential use for specific behaviors and further our understanding of the driving forces behind habitat selection.

## Methods

The original telemetry study was on the Idaho National Engineering and Environmental Laboratory (INEEL), located - 55 km north of Pocatello, Idaho. The vegetation is typical of a northern cool desert with big sagebrush (*Artemisia tridendata*)-grass communities (Anderson and Holte 1981, Anderson et al. 1996). The habitat map we used was based on two satellite images from 8 May 1987 and 17 August 1989. Pixel size was 30 x 30 m. The map was extensively ground checked and corrected in 1990 (Anderson et al. 1996). We used nine vegetation classifications, as defined by Anderson et al. (1996), for our analysis (Table 1).

The telemetry data for this analysis came from the study of Laundré and Keller (1981) conducted in 1976-79. The data consisted of 69 24-hr monitoring blocks from 20 animals (9 females and 11 males). Each 24-hr monitoring block consisted of sequential relocations taken every 15 min. In the original study, the sample animals (n =20) were a random subset of over 80 collared animals and were well distributed around the INEEL. Except for one mated pair, their home range areas did not overlap. Thus we considered the samples to be statistically valid for the analyses we used to test the predictions. The location error for the system of this study was ± 140 m. To incorporate this error, we included a 300 m buffer (150 x 150m) around telemetry locations and movement trajectories when we overlaid them on the habitat map.

We used similar preliminary map procedures to test if coyotes selected specific habitat types for their overall home range area (Prediction 1) and for different types of movement (B and C) within the home range area (Prediction 2). In both cases, we first defined home range areas of coyotes by the grid method (Laundré and Keller 1981) with 30 x 30 m grid cells. We estimated levels of use (time spent, distance traveled, and velocity) within each grid cell based on the 15-min sequential relocations over 24-hr monitoring blocks and then used these estimates to assign use types to each cell. Laundré and Keller (1981) demonstrated that a minimum of five 24 hr monitoring blocks were needed to adequately define a coyote's home range. Consequently, we only used data for five females and three males with five or more such time blocks (range: 5-10) for the home range area analyses.

We estimated habitat makeup of the home range areas by first constructing raster image files of the areas (30 x 30 m pixels) based on telemetry relocations. We georeferenced each of these image files to the habitat image based on the UTM coordinates of the original telemetry data. For each

TABLE 1. Vegetation classes from INEEL vegetation map used in the analyses of this study. Classification and descriptions are based on Anderson et al. (1996).

| Habitat Class (ha) | Description |
|---|---|
| Basin Wildrye (BW) (735) | Near pure stands of Great Basin wildrye (*Leymus cinereus*) |
| Steppe Grassland (SG) (2,880) | Mixture of rhizomatous grasses (e.g. *Pascopyrum smithii*), bunchgrasses (e.g.*Oryzopsis hymenoides*), and shrub species (e.g. *Artemisia* spp.) |
| Grasslands (G) (11,065) | Areas dominated by rhizomatous grasses, bunchgrasses, or crested wheatgrass (*Agropyron desertorum*). |
| Sagebush-Steppe off Lava (SS-off) (85,892) | Non volcanic soils with shrub-grass communities dominated by sagebrush. |
| Sagebrush- Steppe on Lava (SS-on) (90,366) | Areas of basaltic uplands with shrub-grass communities dominated by sagebrush. |
| Sagebrush - Winterfat (SW) (9,208) | Communities dominated by Wyoming big sagebrush and winterfat (*Krascheninnikovia lanata*). |
| Salt Desert Shrub (SD) (7,184) | Various salt desert shrubs primarily saltbrush (*Atriplex falcata*) and shadscale (*A. confertifolia*) |
| Sagebrush - Rabbitbrush (SR) (14,292) | Dominated by a mixture of sagebrush and green rabbitbrush (*Chrysothamnus viscidiflorus*). |
| Low Sagebrush/Rabbitbrush (SR-low) (1,531) | Areas of low growing (usually on lava) shrubs, primarily sagebrush (*Artemisia* spp.) and green rabbitbrush. |

animal, we overlaid the home range image on the habitat image and made a section (windowed image) encompassing the home range area with a 300 m buffer to account for telemetry error (Figure 1a). The total windowed image was the area available to a coyote and the delineated home range was the area coyotes selected. We estimated the habitat makeup (total number of pixels per habitat type) of the total windowed image and, later, the home range area, with the histogram function of the IDRISI software. This function sums the number of pixels of each habitat type in the selected images.

## Prediction 1

In testing prediction 1 (habitat characteristics within the home range will differ from surrounding areas), we tested to determine if the areas selected by coyotes for their home range differed in habitat from what was available in the whole area (home range included) within the 300 m buffer around the home range. We used a G-test (Sokal and Rohlf 1981) and calculated the number of expected pixels within the home range area from the proportion of each habitat type within the total image. We used the number of pixels of each habitat type within the home range boundary as the observed values. The null hypothesis was that use of all habitats was in proportion to their availability. Because not all coyotes had the same habitat composition available (Table 2), we used the individual coyotes as the sample units and calculated separate G-tests for each individual.

## Prediction 2

For Prediction 2 (within the home range, areas of type B and C movement will differ in habitat types), we used the same animals as in Prediction 1 (n = 8) and distinguished cells where animals used either types B or C movements with different cell values. We then separated each group of cell types from the rest of the home range cells with the use of boolean images (Eastman 1992). To construct a boolean image, we assigned 1.0 to all the desired cells (a given movement type) and 0.0 to all undesired cells. We overlaid these images (image 1 x image 2) on the original windowed image and obtained a final habitat image for a particular movement type (Figures 1b & 1c). In such an overlay, all desired cells retain their original

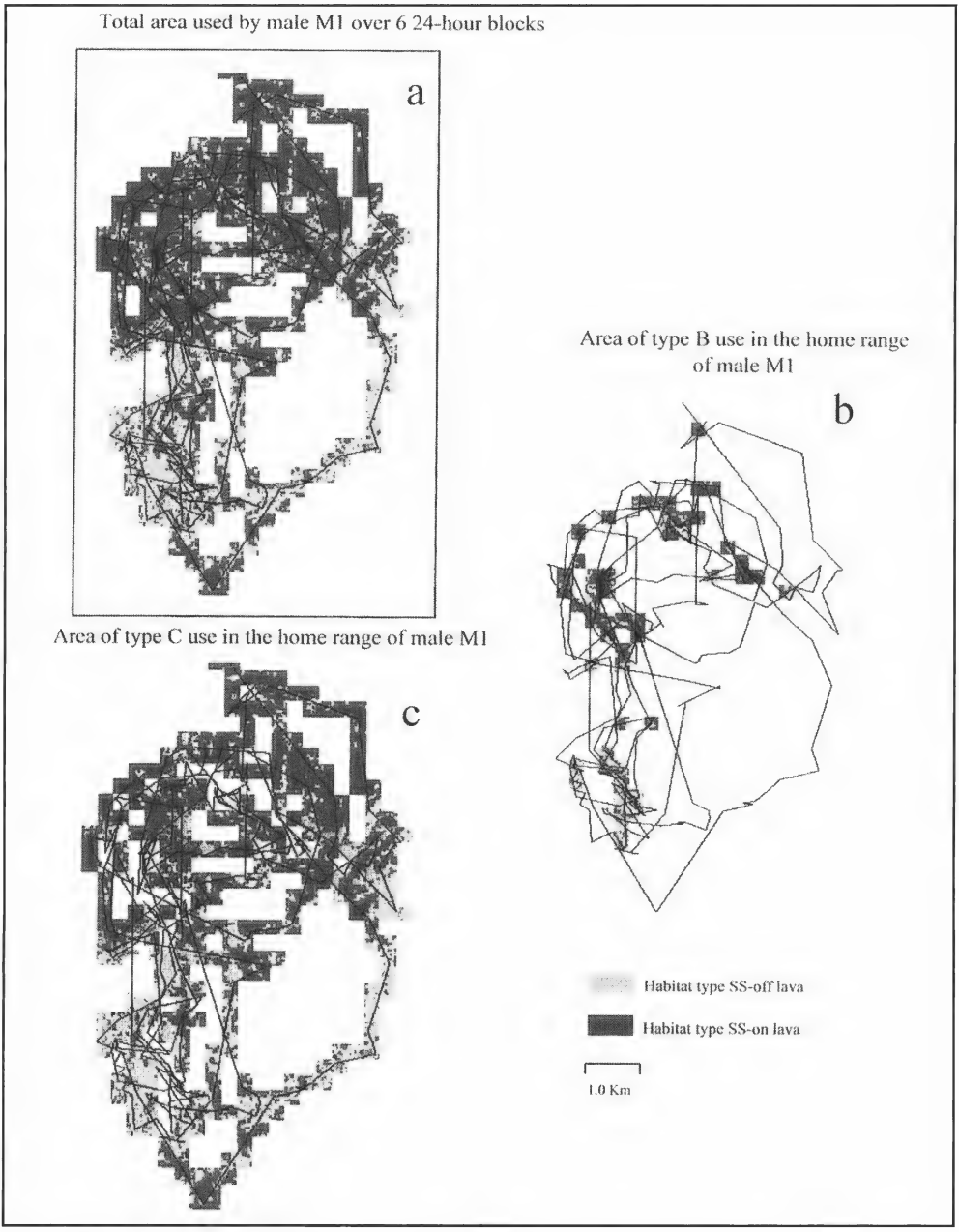
Total area used by male M1 over 6 24-hour blocks
a
Area of type B use in the home range of male M1
b
Area of type C use in the home range of male M1
c
Habitat type SS-off lava
Habitat type SS-on lava
1.0 Km

Figure 1. Demonstration of how habitat composition of the home range area (1a) and areas of type B (1b) and C (1c) use were determined. Once separated, the number of 30 x 30 m pixels of each habitat type were calculated with IDRISI software. The habitat of the total area encompassed by the border around 1a (including the defined home range) was used as the estimate of available habitat for testing the prediction of habitat selection for the home range area (Prediction # 1). For clarity, only the two most abundant habitat types are depicted here.

TABLE 2. Availability (percent of total in area) of the habitat types in the home range of each individual coyote used to test predictions 1 and 2; M = male, F = female. Habitat codes are explained in Table 1.

| Habitat | Coyote ID number M-1 | M-2 | M-3 | F-1 | F-2 | F-3 | F-4 | F-5 |
|---|---|---|---|---|---|---|---|---|
| BW | 0.6 | 0.5 | 0.5 | 1.1 | 0.1 | 0.2 | 1.6 | 0.0 |
| SG | 0.5 | 3.0 | 1.0 | 3.1 | 0.8 | 0.0 | 2.9 | 0.5 |
| G | 1.8 | 7.5 | 5.8 | 8.3 | 6.5 | 2.2 | 11.2 | 2.0 |
| SS-off | 31.0 | 38.2 | 11.2 | 32.5 | 33.0 | 55.4 | 49.2 | 27.3 |
| SS-on | 60.8 | 36.4 | 80.1 | 34.5 | 37.7 | 30.3 | 7.5 | 1.2 |
| SW | 0.5 | 1.2 | 0.1 | 1.1 | 3.7 | 6.5 | 4.3 | 25.5 |
| SD | 0.1 | 1.8 | 0.0 | 2.3 | 6.3 | 1.5 | 3.2 | 16.5 |
| SR | 1.0 | 2.5 | 0.2 | 1.7 | 6.0 | 2.1 | 6.7 | 18.3 |
| SR-low | 1.8 | 1.1 | 0.5 | 1.3 | 3.5 | 0.1 | 0.0 | 0.0 |

value (multiplied by 1.0) and all undesired cells revert to a value of 0.0. Again, we obtained habitat composition of each movement type areas with the histogram function.

To compare if habitat composition differed between areas of type B and C movement, we first conducted a Principal Components Analysis (PCA) (Manly 1994) with the combined data of both movement types. We used a PCA because it effectively incorporated the contribution of multiple variables (via component loadings) of a given entity (i.e., area of specific movement type) and reduced them to one value (Z score) that described the entity. We then compared the Z scores for the appropriate treatments (type B and C movements) with univariate parametric statistical designs or their non parametric equivalents to determine if there were significant differences in habitat composition. The nine variables for the PCA were the percentages of each habitat type (Table 1) for each of the two movement types per animal. We used the resulting loadings for each variable to calculate $Z_1$ and $Z_2$ scores for the two types of areas of use for each animal. We compared the resulting $Z_1$ and $Z_2$ scores in a paired design with types B and C movement being the treatments and the different animals being the eight replicates. The null hypotheses were the mean differences in $Z_1$ or $Z_2$ scores between types B and C movement were not significantly different from zero.

## Predictions 3, 4, and 5

To test Prediction 3 (habitats coyotes used for B and C movements differed during 24-hr travel) we used the telemetry data (15-min locations) for each of the 69 individual 24-hr monitoring blocks we had for the 20 coyotes. For each block, we constructed a grid area similar to the home range grid area. However, in this case the grid cells defined an area used by the coyote during its 24-hr movements (daily range). As with the home range area, we assigned each cell a value for movement type (B or C) based on time spent, distance traveled, and velocity values for each. We then used the cells of these daily ranges to generate a raster image containing these use values. We georeferenced this daily range image to the habitat image and overlaid it on this image. We again separated the cells with different movement types with boolean images to obtain just those cells with either type B or type C movements. Finally, we calculated the habitat composition with the histogram function.

The result of the above analyses produced estimates of habitat composition for types B and C movements for each of the 69 24-hr monitoring blocks of the animals. We used the data for the two types of movements in a PCA that used the percentages of the different habitats as the variables. We used the loadings from this analysis to generate $Z_1$ and $Z_2$ scores for both type B and C areas for each 24-hr monitoring block. To avoid pseudoreplication for those animals for which we had more than one 24-hr monitoring block, we summed and averaged the replicate samples of animals, resulting in 20 individual paired component estimates (Z scores) of areas used for type B and C movements within a 24 hr block. Finally, we compared these paired estimates within a component ($Z_1$ or $Z_2$) with a paired-*t* design. The null hypotheses tested was the mean difference

in paired scores of areas used for types B and C movements for the first or second principal component was not significant from zero.

We tested Prediction 4 (the sexes should use habitat differently for the two movement types) with a two-way ANOVA design for $Z_1$ and $Z_2$ scores with movement type (B and C) and sex as the two levels. As we had tested differences in movement types with the more sensitive paired-t design (Prediction 3 above), here we used movement type primarily as a block (Sokal and Rohlf 1981) to test the main null hypotheses that the mean $Z_1$ nor $Z_2$ scores for these movement types did not differ significantly between males and females.

To test Prediction 5 (seasonal difference in daily habitat use), we used the 69 total daily range habitat images (i.e. total cells entered during a 24 hr block). As before, the percentages of each habitat from the daily ranges were the variables in a PCA with the 69 24-hr monitoring blocks being the replicates. We used the loadings for each variable to generate $Z_1$ and $Z_2$ scores for each block. We separated the $Z_1$ and $Z_2$ scores based on sex and season. We used the seasonal breakdown of Smith et al. (1981) with the following modifications: pair formation (Dec 1- Jan 31; 6 males, 4 females), gestation (Feb 1- Mar 15; 2 males, 3 females), and pup rearing (Mar 16- Aug 31; 7 males, 5 females) (Laundré and Keller 1984). We had no sample blocks for the dispersal season (Sept 1 - Nov 30). We used a two-way ANOVA design (sex x season) to test the null hypothesis that a mean component score ($Z_1$ or $Z_2$) did not differ significantly between sexes nor among seasons. Again, to avoid pseudoreplication, we calculated the means of those animals that were represented by two or more 24-hr monitoring blocks within a given season. We used these mean values for these animals within their appropriate sex x season cell. Thus, each animal within a sex x season cell was only represented by one Z score.

We did all image processing and analyses with IDRISI32 software (Release 2, Clark Lab., George Perkins Marsh Institute, Clark University, Worcester, MA). For the principle component analyses we used Systat software (Version 5.02, Systat, Inc. Evanston IL) and for all statistical tests we used Sigmastat software (Version 2, Jandel Corp., San Rafael, CA). Means are ± standard error and significance levels were $P \leq 0.05$.

## Results

Regarding Prediction 1, habitats sagebrush-steppe off lava (SS-off) and sagebrush-steppe on lava (SS-on) were the most abundant available habitats for all animals, with the exception of coyote F5 where SS-off and sagebrush-winterfat (SW) predominated (Table 2). All eight coyotes selected for specific habitats ($P < 0.001$) (Table 3), thus supporting Prediction 1. The most selected habitat types were SS-off and SS-on (six of eight coyotes). Although one or both of these habitats were also abundant within the home ranges of the other two coyotes, M1 selected low sagebrush/rabbitbrush (SR-low) and F5 selected sagebrush-winterfat (SW).

Relative to the PCA analysis for prediction 2 (B and C movement areas within the home range areas correspond to different types of habitats), the first and second principal components explained

TABLE 3. G-test values to determine if coyotes (M = males, F = females) selected different kinds of habitat.Those values with asterisks were used significantly ($P \leq 0.05$) more (+) or less (-) than available.Habitat codes are explained in Table 1.

| | Coyote ID number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Habitat | M-1 | M-2 | M-3 | F-1 | F-2 | F-3 | F-4 | F-5 |
| BW | 102.5 | -24.6 | -45.9 | -117.0 | 1.8 | 24.6 | -161.2 | -0.6 |
| SG | 91.6 | 166.6 | -21.9 | -122.4 | -64.9 | -3.0 | -151.3 | -39.2 |
| G | 145.3 | 156.5 | -508.5* | -427.8* | -41.3 | -93.4 | -780.4* | -41.1 |
| SS-off | -469.9* | 971.6* | -911.9* | 784.2* | -1258.4* | 200.3* | 1953.9* | -1084.6* |
| SS-on | -154.8 | -1048.9* | 2524.5* | 321.0 | 2216.9* | -69.5 | 675.5* | -31.5 |
| SW | -3.4 | -99.2 | 1.6 | -56.2 | -337.3 | -239.6* | -430.9 | 1072.7* |
| SD | 29.3 | -40.8 | -1.9 | -187.3 | -452.4 | 88.9 | -267.2 | 234.6 |
| SR | -9.4 | 126.7 | -10.4 | 21.8 | -182.2 | 179.4* | -681.6* | 136.4 |
| SR-low | 407.8* | -29.9 | 46.6 | 3.0 | 824.9 | 4.2 | 0.8 | 0 |

61.8% of the total variance (Table 4). When we tested if the B and C movement areas correspond to different types of habitats, we used the Wilcoxon signed rank test to compare the $Z_1$ scores calculated from the PCA (Table 4). We found a significant difference ($P = 0.016$) between $Z_1$ scores for type B ($\bar{x} = 0.84 \pm 1.21$) and C ($\bar{x} = -0.84 \pm 1.24$) movement. We found no significant differences for the $Z_2$ scores. The value of a given $Z_1$ is a function of the component loading value and the magnitude of the standardized variable (percent use). As the loadings for each variable were the same for types B and C movements, the differences in $Z_1$ scores reflected habitats that had different percent use between the two movement types; habitats with the same percent use between movements contributed equally to the their $Z_1$ scores. To identify which habitats might be contributing to the differences in $Z_1$ scores, we plotted the percent use of each habitat for types B and C movement (Figure 2) along with their respective component loadings. Since the component loading for habitat SS-on was large (0.807) and positive (Figure 2), the higher $Z_1$ scores for type B movements reflected the higher use of this habitat for type B movement compared to type C movement. Other differences in habitat use contributing to the differences in $Z_1$ scores were higher uses of SS-off (-0.25), SD (-0.81), and SR (-0.93) for type C movements (Figure 2). Habitat type SW had a high negative loading (-0.81) but it was used equally for both movement types.

To test for differences in areas used for types B and C movements within the 24-hr monitoring blocks (Prediction 3), the PCA combined the data relative to types B and C movements within the 69 24-hr monitoring blocks. Percent variance explained by the first and second principal components was 66.3% (Table 4). When we analyzed $Z_1$ scores we found significantly higher ($P < 0.001$) scores in areas coyotes used for type C movement ($0.82 \pm 0.58$) than for type B movement ($0.03 \pm 0.58$) (Figure 3a). Again, there was no significant difference between the two movement types for $Z_2$ values. For the first component, the lower $Z_1$ scores for type B movement compared to type C (Figure 3a) primarily reflected higher use of the SS-on habitat which, in this case, had a high negative loading (Figure 3b) and lower use of the SS-off, G, and SR habitats relative to type C movements (Figure 3b).

When we compared habitat composition of areas used by males and females for types B and C movements during 24 hr (Prediction 4), we found significantly higher $Z_1$ scores for females than males ($P = 0.042$). Again, there was no significant difference for $Z_2$ scores. The difference between sexes for the $Z_1$ scores reflected higher scores for females compared to males for both type B and C movements (Figures 4a, 4c). For both

TABLE 4 . Results of the various principal component analyses conducted to help test predictions #2-5 of this study. Prediction # 2 concerns the difference in habitat makeup of areas of types B and C use within the home range. Differences in habitat of areas used by coyotes in types B and C manner within a 24-hr monitoring block constitutes prediction #3. Prediction # 4 concerns differences in habitat use by males vs females for types B and C movements. Prediction # 5 states that there would be differences in habitat composition during daily use relative to season and sex of coyotes. The component loadings for the first and second principal component and the percent of the total variance explained are given. Component loadings for habitat Basin Wildrye (BW) are not presented because of its low occurrence and use. Habitat codes are explained in Table 1.

| Prediction | | Habitat Type | | | | | | | | % Total Variance |
|---|---|---|---|---|---|---|---|---|---|---|
| | | SG | G | SS-off | SS-on | SW | SD | SR | Sr-low | |
| 2 | $Z_1$ | 0.07 | -0.12 | -0.25 | 0.81 | -0.81 | -0.81 | -0.93 | 0.44 | 33.5% |
| | $Z_2$ | -0.61 | -0.83 | -0.92 | 0.54 | 0.42 | 0.33 | 0.33 | 0.41 | 28.3% |
| 3 & 4 | $Z_1$ | 0.26 | 0.32 | 0.51 | -0.87 | 0.70 | 0.64 | 0.81 | -0.53 | 37.9% |
| | $Z_2$ | -0.68 | -0.70 | -0.62 | 0.29 | 0.56 | 0.51 | 0.46 | 0.28 | 28.4% |
| 5 | $Z_1$ | 0.24 | 0.16 | 0.40 | -0.87 | 0.83 | 0.76 | 0.87 | -0.54 | 41.2% |
| | $Z_2$ | -0.69 | -0.61 | -0.72 | 0.39 | 0.50 | 0.51 | 0.37 | 0.42 | 29.2% |

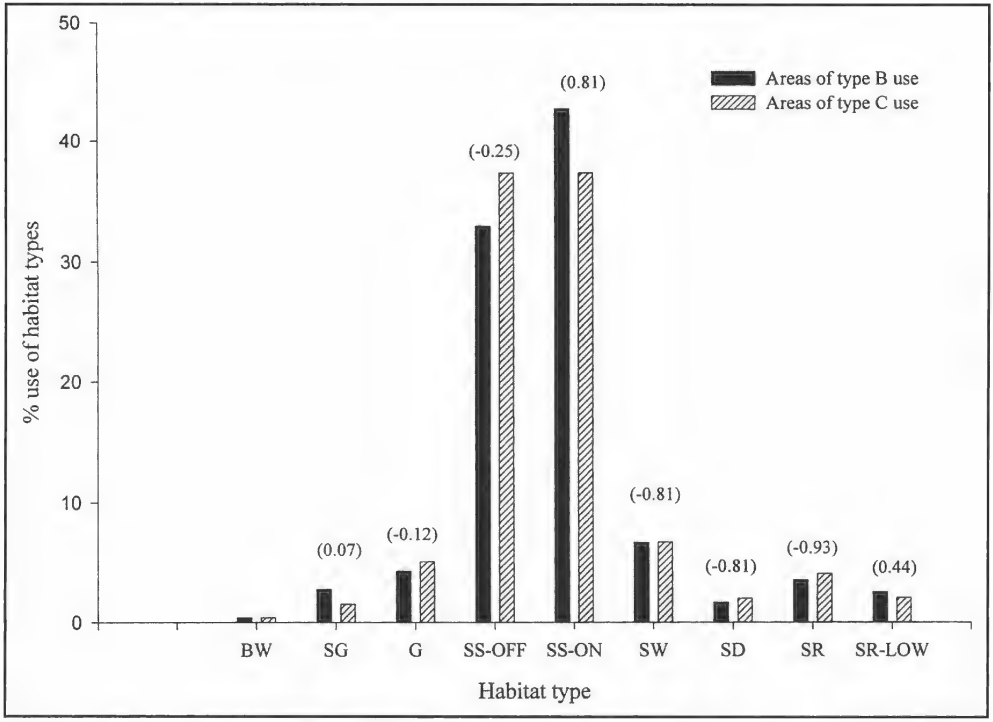


Figure 2. Habitat makeup (percent of total pixels) of areas within the home ranges coyotes used in either a type B or C manner. The component loadings resulting from the PCA are included for the eight most used habitats.

movements types, the higher $Z_1$ scores for females reflected lower use of SS-on and higher use of SS-off, SR, SD, and SW habitats when compared to males (Figures 4b, 4c). Basically, females used a wider range of habitat types than males for both types B and C movements.

Finally we also saw differences in habitat composition, as expressed by $Z_1$, of areas coyotes used daily relative to season ($P = 0.04$) and sex ($P = 0.03$) (Prediction 5). Again, there was no significant difference for $Z_2$ scores. Relative to seasons, the mean $Z_1$ score for pair formation ($1.5 \pm 1.01$) was significantly higher than for gestation ($-2.16 \pm 0.77$) with pup rearing ($0.14 \pm 0.94$) being intermediate between the other two (Figure 5a). An analysis of the component loadings for these PCAs and percentages of seasonal use (Figure 5) indicated lower $Z_1$ scores (Figure 5a) reflected a selection for habitat type SS-on and higher scores reflected higher uses of habitats G, SS-off, SW, and SR (Figure 5b). This means coyotes in general were switching habitat use with a more diverse use of habitats during pair formation, a switch to higher uses of SS-on during gestation and then increasing again the use of other habitats during pup rearing.

Relative to the significant difference between sex, sample sizes were small but still indicated that the overall seasonal mean $Z_1$ score for females ($1.6 \pm 1.10$) was significantly higher than for males ($0.88 \pm 0.50$). The differences in $Z_1$ scores between sexes within seasons (Figures 6a, 6c, 6e) reflected a more diverse selection of habitats by females during pair formation (Figure 6b) and a higher use of SS-on (high negative loading) by males. During gestation (Figure 6d) both sexes concentrated their activity on SS-on and SS-off habitats but in different proportions; females used SS-off more whereas males used SS-on habitats more. During the pup rearing season, females again diversified their habitat use (Figure 6f) whereas males continued using the SS-on habitat.

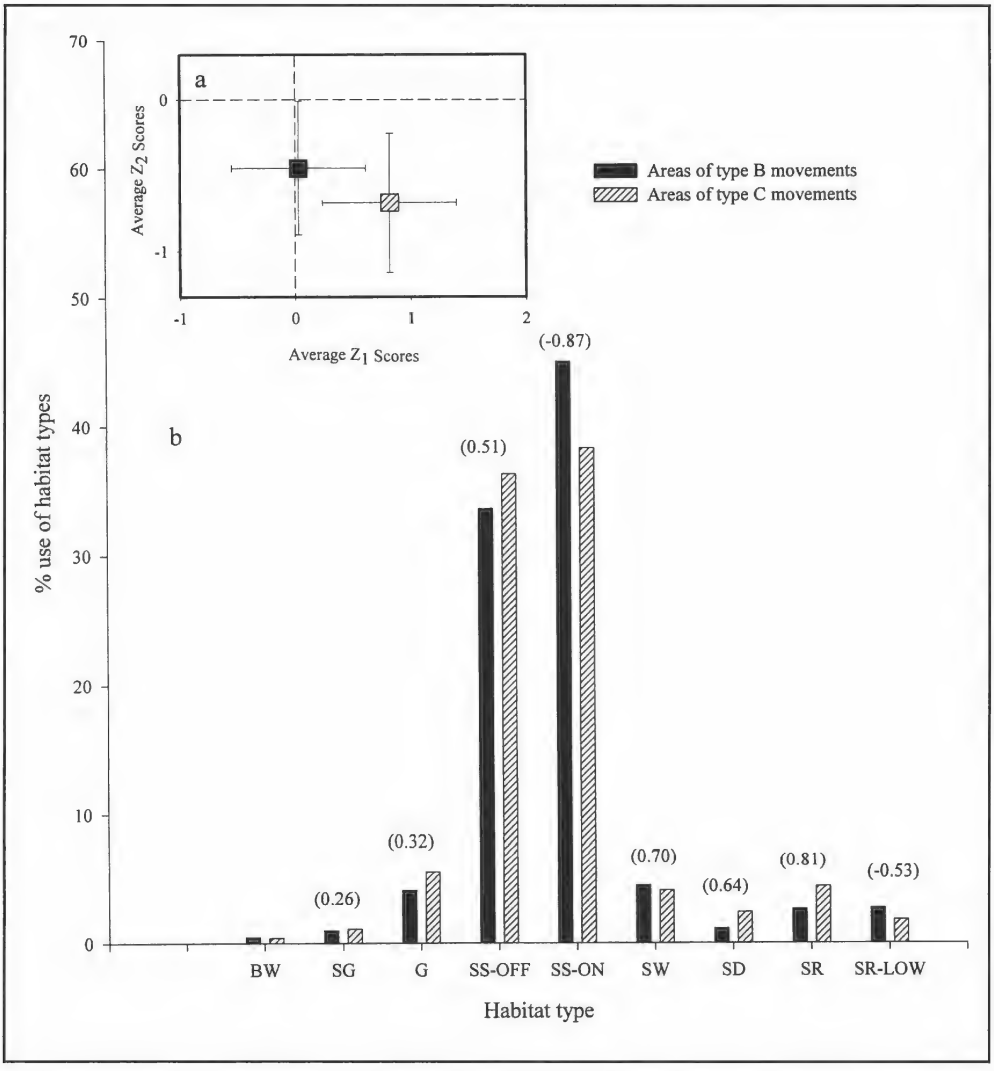


Figure 3. Plot of the $Z_1$ and $Z_2$ scores for areas of type B and C movements within the 24-hr time blocks (3a). Figure 3b is the habitat makeup (percent of total pixels) of areas within the 24-hr monitoring block where coyotes used type B and C movements. The component loadings resulting from the PCA are included for the eight most used habitats.

## Discussion

Although the small sample size of our study (eight animals) may limit interpretation of our results, there is an indication that coyotes in our study area exhibited selection for specific habitats in defining their home range area. Additionally, we found the home range area likely has a basis in the daily use of the back and forth and ranging movement types by coyotes (Figure 2). Because we defined coyote home range areas based on 24-hr monitoring blocks, this might be expected. However, areas would be designated for a given movement type only if its use predominated there. Thus, the use of the 24-hr monitoring blocks

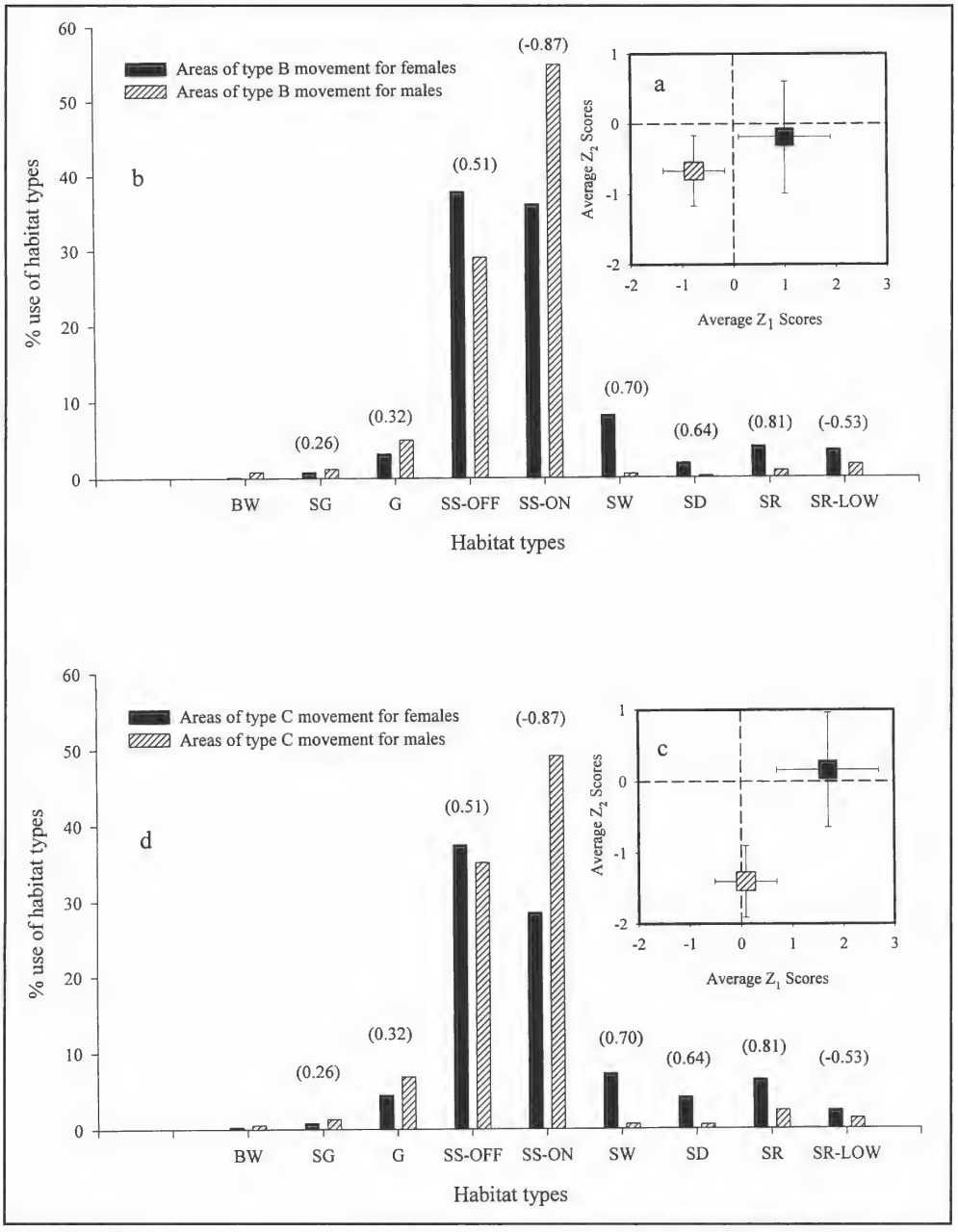


Figure 4. Plots of the $Z_1$ and $Z_2$ scores for female and male coyotes relative to types B (4a) and C (4c). Figures 4 b & d depict the habitat makeup (percent total pixels) of the areas female and male coyotes used for type B (4b) and C (4 d) movements within the 24-hr monitoring block. The component loadings resulting from the PCA are included for the eight most used habitats.

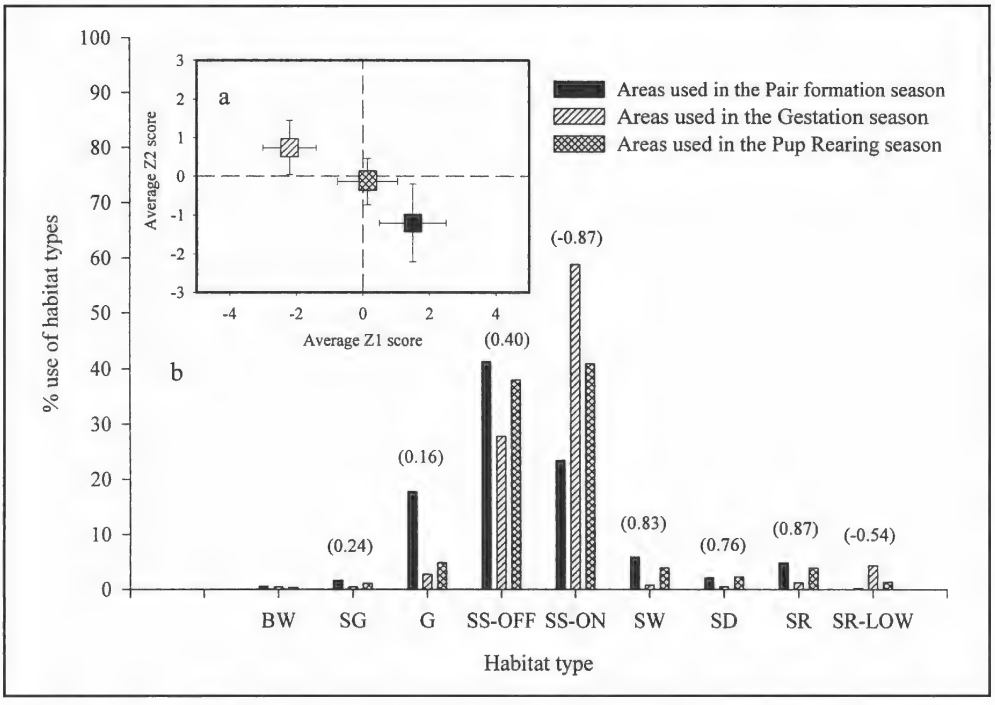


Figure 5. Plots of the $Z_1$ and $Z_2$ scores for areas used by coyotes for the three seasons: pair formation, gestation, and pup rearing (5a). Figure 5 b is of the habitat makeup (percent of total pixels) of areas coyotes used in 24-hours during the three seasons of pair formation, gestation, and pup rearing. The component loadings resulting from the PCA are included for the eight most used habitats.

delineates the home range area on a behavioral basis rather than merely a polygon containing a series of dots. The result is a home range area that represents how coyotes integrate their daily movements within the available habitats.

Our findings for Predictions 4 and 5 supported the hypothesis that habitat use should differ between sexes and among seasons and again, not only showed sexual differences and seasonal changes in habitat use, but also linked these differences to changes in behavior. For example, seasonal and sexual differences in the uses of types B and C movements (Laundré and Keller 1981) corresponded to shifts in the habitat composition of areas used for these movements (Figures 5,6). However, because of limited sample sizes in some sex x season categories, these results should be interpreted cautiously. Additional data in this area would help clarify these relationships.

The idea of habitat selection by coyotes is not new (Ozoga and Harger 1966, Gipson and Sealander 1972, Berg and Chesness 1978, Andelt and Gipson 1979, Litvaitis and Shaw 1980, Roy and Dorrance 1985, Gese et al. 1988, Holzman et al. 1992, Hernández et al. 1993, Murry et al. 1994). However, in most other studies, coyotes often selected among quite discrete habitats (wheat fields vs. pasture). Hernández et al. (1993) were some of the first to demonstrate that fine habitat characteristics (e.g. shrub density and topographic features), may influence coyote habitat use. Our results concur with those of Hernández et al. (1993) and we now have ample data that coyotes exhibit preferences in habitat use ranging from areas containing discrete vegetational patterns to those where habitats change in more subtle ways.

Given that coyotes do select habitat combinations based on their different use of these areas,

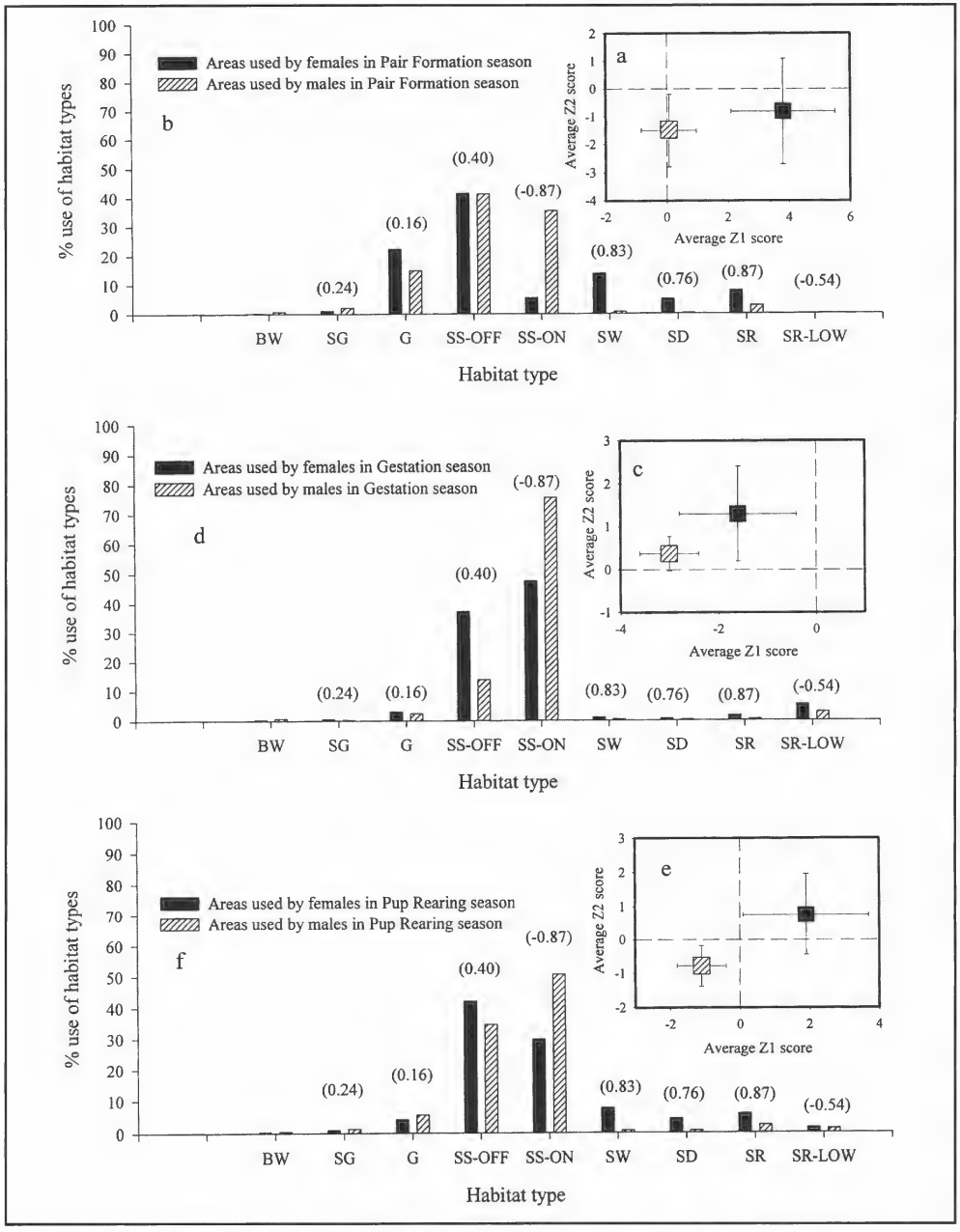


Figure 6. Plots of the $Z_1$ and $Z_2$ scores for males and females for each of the three seasons, pair formation (6a), gestation (6c) and pup rearing (6e). Figures 6 b, d, & f are of the habitat makeup (percent of total pixels) of areas female and male coyotes used in 24-hours during the pair formation, gestation, and pup rearing seasons. The component loadings resulting from the PCA are included for the eight most used habitat.

the questions still remains as to why? Optimal foraging theory predicts predators will make habitat use (patch) decisions based primarily on food availability and ease of capture (Brown et al. 1999). Hernández et al. (2002) have demonstrated that coyotes incorporate optimal foraging approaches in their diet selection. Also, others have demonstrated that prey in response to predation risk will alter their behavior and habitat use patterns (Laundré et al. 2001, Altendorf et al. 2001, Marín et al. 2003). Within this landscape of fear created by predation risk (Laundré et al. 2001), composition and densities of coyote prey will vary among habitats (Murry et al. 1994, Marín et al. 2003) and capture success can differ relative to habitat type (Murry et al. 1994, Gese et al. 1995). This produces an inverse landscape of opportunity for coyotes relative to prey capture. If the two movement types represent different hunting patterns then one hypothesis is that coyotes of this study exhibit differing hunting behaviors in various parts of their home range because of different prey composition/density/catchability found there.

Further research needs to test the link between behavioral use of a habitat type and prey composition and how well optimal foraging theory might explain movement patterns and habitat selection by coyotes. If these models are supported by future research, we will then have a deeper understanding of the driving forces behind habitat preferences in coyotes. This increased understanding could help us in our effort to manage our coexistence with this ubiquitous predator, specifically in rangeland areas where conflicts are frequent.

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## Literature Cited

Altendorf, K. B., J. W. Laundré, C. A. López González, and J. S. Brown. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430-439.

Andelt, W. F., and P. S. Gipson. 1979. Home range, activity, and daily movements of coyotes. Journal of Wildlife Management 43:944-951.

Anderson, J. E., and K. E. Holte.1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. Journal of Range Management 34:25-29.

Anderson, J. E., K. T. Ruppel, J. M. Glennon, K. E. Holte, and R. C. Rope. 1996. Plant communities, ethnoecology, and flora of the Idaho National Engineering Laboratory. Unpublished report ESRF-005 Environmental Science and Research Foundation, Idaho Falls, Idaho.

Berg, W. E., and R. A. Chesness.1978. Ecology of coyotes in northern Minnesota. Pages 229-247 *In* M. Bekoff (editor), Coyotes: Biology, Behavior, and Management. Academic Press, New York.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear; optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80: 385-399.

Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 *In* M. Bekoff (editor), Coyotes: Biology, Behavior and Management. Academic Press, New York.

Chesness, R. A., and T. P. Bremicker. 1974. Home range, territoriality and sociability of coyotes in northcentral Minnesota. Paper presented at 1974 Coyote Workshop, Denver, Colo. Minnesota Department of Natural Resources, Grand Rapids, Minnesota.

Eastman, J. R. 1992. Idrisi. Technical reference. Version 4.0. Clark University, Worcester, Mass.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management 52:640-646.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1995. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. Canadian Journal of Zoology 74:784-797.

Gipson, P. S., and J. A. Sealander. 1972. Home range and activity of the coyote (*Canis latrans frustror*) in Arkansas.Pages 82-95 *In* Proceedings of the 26th Annual Conference of Southeastern Association of Game and Fish Commissioners, Nashville, Tennessee.

Hernández, L., M. Delibes, and E. Ezcurra. 1993. Activity pattern, home range, and habitat preference by coyotes (*Canis latrans*) in the Mapimi Biosphere Reserve of the Chihuahuan Desert, Mexico.Doñana, Acta Vertebrata 20:276-282.

Hernández, L., R. R. Parmenter, J. W. Dewitt, D. C. Lightfood, and J. W. Laundré. 2002. Coyote diets in the Chihuahuan Desert, more evidence for optimal foraging. Journal of Arid Environments51:613-624.

Holzman, S., M. J. Conroy, and J. Pickering. 1992. Home range, movements, and habitat use of coyotes in southcentral Georgia. Journal of Wildlife Management 56:139-146.

Laundré, J. W., and B. L. Keller. 1981. Home-range use by coyotes in Idaho. Animal Behaviour 29:449-461.

Laundré, J. W., and B. L. Keller. 1984. Home-range of coyotes: a critical review. Journal of Wildlife Management 48:127-139.

Laundré, J. W., and R. J. Wilkosz. 1991. The use of cluster analysis to analyze habitat use by coyotes in an area

of low vegetal heterogeneity. Northwestern Naturalist 72:12-20.
Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79:1401-1409.
Litvaitis, J. A., and J. H. Shaw. 1980. Coyote movement, habitat use, and food habits in southwestern Oklahoma. Journal of Wildlife Management 44:62-68.
Manly, B. F. J. 1994. Multivariate Statistical Methods: a Primer. 2nd edition. Chapman and Hall, London, U.K.
Marín, A. I., L. Hernández, and J. W. Laundré. 2003. Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*): an optimal foraging approach. Journal of Arid Environments. 55:101-110.
Murry, D. L., S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. Canadian Journal of Zoology 72:1444-1451.

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Oehler, J. D., and J. A. Litvaitis. 1995. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070-2079.
Ozoga, J. J., and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. Journal of Wildlife Management 30:809-379.
Person, D. K., and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. Journal of Wildlife Management 55:433-441.
Roy, L. D., and M. J.Dorrance. 1985. Coyote movements, habitat use, and vulnerability in central Alberta. Journal of Wildlife Management 49:307-313.
Smith, G. J., J. R. Cary, and O. J. Rongstad. 1981. Sampling strategies for radio-tracking coyotes. Wildlife Society Bulletin 9:88-93.
Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Freeman. San Francisco, California.

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# Demography of Montane Voles in Old Field and Orchard Habitats in Southern British Columbia

## Abstract

Voles occupy perennial grasslands and agricultural areas in many parts of North America. This study was designed to provide a detailed analysis of the population dynamics of montane voles in old field and orchard habitats. Vole populations were intensively live-trapped in replicate old field and orchard sites over a 4-yr period at Summerland, British Columbia. Populations of montane voles reached peak densities of 186 and 144 voles/ha in old field sites before declining to numbers averaging <60 voles/ha. Orchard populations of montane voles also followed this pattern but at consistently lower numbers than old field sites. This difference in abundance ranged from 2.3-3.6 times during the peak year to 23.8-116.3 times in the decline year, at which time montane voles had declined to a mean number of 0.3-2.4 voles/ha in orchard sites. Length of breeding seasons, proportion of reproductive voles, and mean number of recruits were generally similar in old field and orchard sites. Overall mean survival of voles tended to decline through time in orchard sites, averaging 0.47 compared with old field survival of 0.76. Mean body mass of voles was consistently higher in old field than orchard sites. Montane vole populations in orchards seemed to be linked to source area dynamics of populations in old fields.

## Introduction

Populations of voles (*Microtus* spp.) fluctuate in abundance every 2 to 5 yr in North America (Krebs and Myers 1974, Taitt and Krebs 1985). These rodent species prefer perennial grassland habitats that provide both cover and food sources such as grasses, sedges, and forbs (Reich 1981, Getz 1985). Multi-annual population fluctuations appear to require a minimum level of vegetative cover to generate increases in abundance of voles (Birney et al. 1976).

The montane vole (*M. montanus*) is distributed throughout the central cordilleran region of western North America (Banfield 1974). This species appears to prefer arid short grassland in high elevation alpine meadows in the southern part of its range, but it occurs at lower elevations and in valley bottoms towards the northern extent of its range (Banfield 1974). The montane vole is similar to the meadow vole (*M. pennsylvanicus*) in many of its habits with some limited evidence reported for both multi-annual and annual cycles of abundance (Negus et al. 1986, Pinter 1986, 1988). Based on the review of Taitt and Krebs (1985), the montane vole is the least studied microtine of all the major vole species in North America.

Montane voles and meadow voles are the most common microtine species affecting tree fruit production in western North America (Godfrey 1986, Sullivan and Hogue 1987, Askham 1988). The meadow vole and pine vole (*M. pinetorum*) cause similar damage to orchards in the eastern part of the continent (Byers 1984). Apple (*Malus domestica*) trees are particularly susceptible to feeding damage during winter periods when voles feed on bark, vascular tissues, and roots. This damage may lead to direct mortality from girdling or reduced growth and yield from sub-lethal feeding (Pearson and Forshey 1978).

There is a dearth of intensive population studies of voles in orchard habitats. Previous work reported that fine-textured soils limited the distribution of pine voles (Fisher and Anthony 1978), invasion of voles from nearby fields caused a rapid increase in vole populations (Horsfall 1964), and voles responded negatively to herbicide-induced weed control in orchard agro-ecosystems (Sullivan et al. 1998, 2000, Merwin et al. 1999). Thus, this study was designed to determine the abundance and population fluctuations of montane voles in old field and orchard ecosystems, with respect to variability between habitats, seasons, years, and the interactions of these factors.

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## Methods

### Study Area and Experimental Design

This study was conducted from 1982-1986 at the Pacific Agri-Food Research Centre in the Okanagan Valley, Summerland, British Columbia. The experimental design consisted of two old field and two orchard habitats. The old field habitats were abandoned (≥25 yr) hay fields composed of crested wheatgrass (*Agropyron cristatum*), quack grass (*Agropyron repens*), downy brome (*Bromus tectorum*), diffuse knapweed (*Centaurea diffusa*), with some minor forbs such as yellow salsify (*Tragopogon dubius*), great mullein (*Verbascum thapsus*), American vetch (*Vicia americana*), prickly lettuce (*Lactuca serriola*), and tall tumblemustard (*Sisymbrium altissimum*). Both old field sites were each 2 to 3 ha within a mosaic of sagebrush (*Artemisia tridentata*), ponderosa pine (*Pinus ponderosa*) forest, and orchard habitats. These old fields had resident populations of montane voles and a few long-tailed voles (*M. longicaudus*). Other species included the deer mouse (*Peromyscus maniculatus*), northwestern chipmunk (*Tamias amoenus*), Great Basin pocket mouse (*Perognathus parvus*), and western harvest mouse (*Reithrodontomys megalotis*).

The two orchards were: (1) a 5-yr-old apple orchard unit and (2) a 10-yr-old apple orchard combined with a 15-yr-old pear (*Pyrus* sp.) orchard as one unit. Both 1.2-ha orchards were located within a 90-ha mosaic of fruit trees and vineyards. Our experimental design had two replicate blocks, each consisting of one old field site and one orchard site. Each pair of old field and orchard sites was spatially segregated to enhance statistical independence (Hurlbert 1984). Common grass species on the orchard sites included orchard grass (*Dactylis glomerata*), quack grass, bluegrass (*Poa* spp.), smooth brome (*Bromus inermis*), and crested wheatgrass. These orchards were mowed 5-6 times each summer. Montane voles were the major microtine species with deer mice and northwestern chipmunks also present. Rodenticides were applied 3-4 times each winter in poison-bait feeder stations.

### Vole Populations

All voles were live-trapped on 1-ha grids with 49 (7 x 7) trap stations located at 14.3-m intervals with 1-2 Longworth live-traps at each station. When capture success exceeded 80% of the 49 traps on a grid, an additional trap was added at each station to prevent trap saturation. One of the old-field grids was an irregular shaped rectangle of 1 ha with 49 stations. The two orchard and two old field grids were live-trapped at 3-wk (spring, summer, and fall) and at 4-6-wk (winter) intervals from June 1982 to April 1986. Trapping effort was the same for all four grids throughout the study.

Traps were baited with whole oats, peanut butter, and carrot; coarse brown cotton was supplied as bedding. Traps were set on day-1, checked on the morning and afternoon of day-2 and morning of day-3, and then locked open between trapping periods. All animals captured were ear-tagged with serially numbered tags, breeding condition noted, weighed on spring balances, and point of capture recorded. The duration of the breeding season was noted by palpation of male testes and the condition of mammaries of the females (Krebs et al. 1969). A pregnancy was considered successful if a female was lactating during the period following the estimated time of birth of a litter. Animals were released on the grids immediately after processing.

Seasons were defined as summer (April to September) and winter (October to March) periods. Thus, there were four summer and four winter periods. We used age at sexual maturity to determine age classes of voles. Body weight was used as an index of age. The percentage of sexually mature animals was used to determine the weight limitations for juveniles, subadults, and adults assuming that juveniles were seldom, if ever, sexually mature; that <50% of the subadults in the upper weight class were mature; and that ≥ 50% of the adults were sexually mature in the lowest weight class. Voles were classified as juvenile (includes juvenile and subadult classes pooled) or adult by body weight (juvenile = 1 – 26 g, adult ≥ 27 g). Juveniles were considered to be young animals recruited during the study. Recruits were defined as new animals that entered the population through reproduction and immigration. All handling of animals was in accordance with the principles of the Animal Care Committee, University of British Columbia.

### Demographic Parameters

Population densities were estimated by the Jolly-Seber (J-S) model (Seber 1982) for reasons in-

dicated by Jolly and Dickson (1983). The J-S model provides the best estimates of population size for mark and recapture data when trappability values are generally < 70% (Hilborn et al. 1976). However, when population size falls low and no marked animals are recaptured, the J-S estimate becomes unreliable and impossible to calculate (Krebs et al. 1986). For these low sample weeks, a minimum number of animals known to be alive (MNA) (Krebs 1966) value was substituted for a biologically unreasonable J-S estimate.

Measurements of recruitment, number of lactating females, and early juvenile survival were derived from the sample of animals captured in each trapping session and then summed for summer periods. Early juvenile survival is an index relating recruitment of young into the trappable population to the number of lactating females (Krebs 1966). We used a modified version of this index, which was number of juvenile animals at week t divided by the number of lactating females caught in week t – 3. Mean survival rates (28-day) for voles in summer and winter periods were estimated from the J-S model. Mean body mass of combined males and females was used as an index of condition within populations of voles during summer and winter periods.

### Statistical Analysis

Our design was a 2x2x4 randomized complete block factorial Model I analysis of variance (ANOVA) (Zar 1999). We had three factors: A was habitat with 2 levels (old field and orchard); B was season with 2 levels (summer and winter); and C was year with 4 levels (1982-83, 1983-84, 1984-85, 1985-86). This analysis was conducted to test differences in mean abundance, mean number of recruits, mean J-S survival, and mean early juvenile survival of voles between old field and orchard sites. For the analyses, a single estimate of the given parameter for each habitat, season, and year was derived to test for differences between the two treatments.

Proportion of adult males and adult females breeding was analyzed by a $\chi^2$ 2 x 2 contingency table (Zar 1999) for each of the four summer periods. These datasets of proportion of animals breeding often include voles captured more than once, and hence they are not completely independent. Thus, the $\chi^2$ analyses provide only an indication of the degree of difference between datasets. Mean J-S survival rates and mean body mass were presented with 95% confidence intervals (CI) to provide a range of measurements for summer and winter periods.

In all analyses, the level of significance was $P = 0.05$.

## Results

### Abundance

We captured 1,877 individual montane voles in two old field and 712 voles in two orchard sites. Mean J-S trappability (susceptibility to capture) estimates ranged from 61.4% to 78.1% (summer) and from 65.0% to 78.7% (winter) in the old field sites. These estimates ranged from 47.0% to 88.9% (summer) and from 28.6% to 85.7% (winter) in the orchard sites.

Old field abundance increased during summer 1982 and winter 1982-83 reaching peak densities of 186 and 144 voles/ha in late fall-early winter 1983 (Figure 1). Montane vole populations in the orchard sites also tended to follow this pattern, but at significantly lower mean numbers than in old field sites ($P < 0.01$) (Table 1). This difference ranged from 1.5-2.9 times in summer 1982 to 23.8-116.3 times in winter 1985-86, by which time montane voles had declined to low numbers (0.3 to 2.4 voles/ha on average) in the orchard sites (Figure 1, Table 1). Numbers in the old field sites declined over winter 1983-84 before peaking again in 1984 at densities of 156 and 146 voles/ha. Vole populations then declined during 1985 and 1986 to numbers averaging < 60 voles/ha (Table 1). The season x year interaction was significant ($P = 0.04$), thereby indicating that the pattern of higher abundance during winter than summer periods was not maintained through time on the orchard sites. No other sources of variance were significant.

### Reproduction and Recruitment

The breeding season for montane voles, based on reproductive condition of adult males, began in February each year and continued until at least October. This pattern was the same in both old field and orchard sites. The proportion of adult females with successful pregnancies ranged from 0.30 to 0.58 in the old field sites and from 0.24 to 0.55 in the orchard sites (Table 2). A significantly greater proportion of adult female voles was

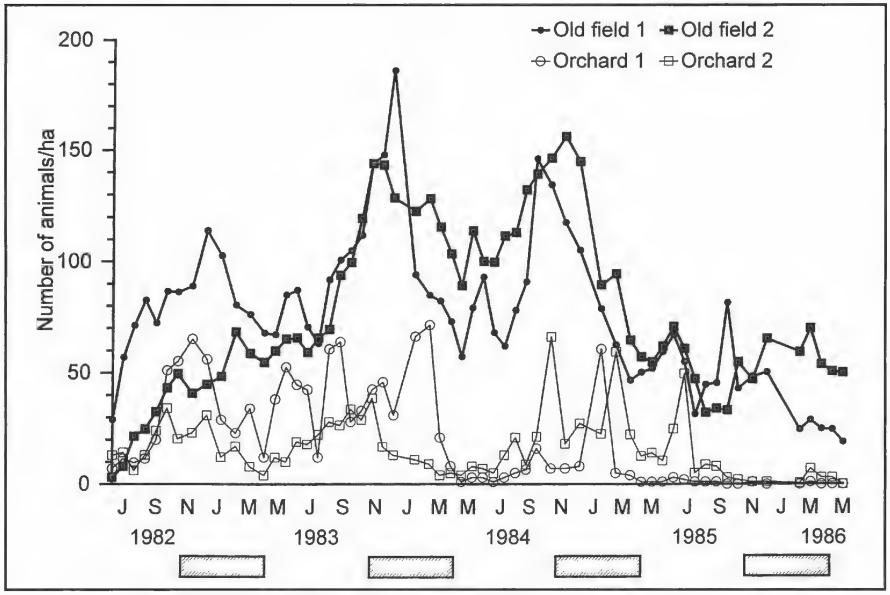


Figure 1. Population densities (Jolly-Seber) per ha of montane voles in replicate old field and orchard sites during the study. Shaded bars indicate winter periods.

TABLE 1. Mean (± SE) abundance per ha for montane voles during summer and winter periods in replicate old field and orchard sites. Sample size ($n$ = number of trapping periods) in parentheses.

| | | Replicate 1 | | Replicate 2 | |
|---|---|---|---|---|---|
| Period | | Old field | Orchard | Old field | Orchard |
| Summer 1982 | (7) | 69.2 ± 7.8 | 23.6 ± 7.8 | 26.0 ± 6.5 | 17.8 ± 3.5 |
| Winter 1982-83 | (5) | 92.4 ± 7.0 | 41.4 ± 8.1 | 52.1 ± 5.0 | 18.2 ± 4.1 |
| Summer 1983 | (9) | 82.0 ± 5.2 | 39.3 ± 6.3 | 70.3 ± 5.2 | 19.3 ± 3.2 |
| Winter 1983-84 | (8) | 115.5 ± 14.1 | 39.8 ± 7.6 | 125.7 ± 4.8 | 15.8 ± 4.3 |
| Summer 1984 | (8) | 84.3 ± 9.9 | 4.8 ± 1.7 | 112.4 ± 5.9 | 11.0 ± 2.4 |
| Winter 1984-85 | (6) | 90.8 ± 13.8 | 15.3 ± 9.1 | 116.1 ± 15.5 | 35.9 ± 8.6 |
| Summer 1985 | (9) | 54.0 ± 4.8 | 1.2 ± 0.3 | 50.1 ± 4.7 | 15.1 ± 4.8 |
| Winter 1985-86 | (7) | 34.9 ± 4.4 | 0.3 ± 0.2 | 57.2 ± 3.1 | 2.4 ± 0.9 |

lactating in the orchard than old field sites in 1984 ($P < 0.01$), with no significant differences between sites in the other years.

Mean number of new voles was not significantly different, between old field and orchard sites, during summer and winter seasons, and over time (Table 3). There were no significant interactions for any of the factors.

## Survival and Body Mass

Mean J-S survival was not significantly different between orchard and old-field sites during summer and winter seasons and over time (Figure 2). The habitat x year interaction approached significance ($P = 0.06$) and this pattern was clearly outlined in the declining survival of voles in orchard sites from 1982 to 1984 (Figure 2). Mean survival of voles was 0.73 ± 0.02 in summer and 0.78 ± 0.02 in winter in old field sites compared with 0.46 ± 0.05 in summer and 0.47 ± 0.05 in winter in orchard sites. An index of early juvenile survival was similar in orchard and old field sites (Table 4). There were no other significant interactions for any of the factors relating to these survival parameters.

TABLE 2. Proportion of adult male (scrotal testes) and female (successful pregnancies) montane voles in reproductive condition during breeding seasons each year for pooled data in replicate old field and orchard sites. Sample size (number of voles) in parentheses. The only significant difference, by $\chi^2$, was for females in 1984.

| Year | Old field | Orchard |
|---|---|---|
| Males | | |
| 1982 | 0.94 (154) | 0.90 (61) |
| 1983 | 0.92 (416) | 0.96 (134) |
| 1984 | 0.92 (525) | 0.94 (48) |
| 1985 | 0.92 (349) | 0.98 (40) |
| Females | | |
| 1982 | 0.30 (251) | 0.24 (100) |
| 1983 | 0.34 (1005) | 0.33 (193) |
| 1984 | 0.31 (969) | 0.47 (68) |
| 1985 | 0.58 (521) | 0.55 (47) |

Mean body mass of montane voles appeared to be higher in old field than orchard sites in most seasons (Figure 3). Old field populations of voles generally had lower mean body masses in winter than summer periods.

## Discussion

### Patterns of Abundance

Our study covered a 4-yr period during an increase, peak, and decline in the cyclic fluctuation of the montane vole, and it is the first detailed comparison of vole population dynamics in old field and orchard habitats. Abundance of voles in the two old field sites ranged from a mean overwinter value in 1982 of 72.3 animals/ha to 120.6 in 1983 and 103.5 in 1984, before declining to 46.1 in 1985.

TABLE 3. Mean (± SE) number of recruits per ha for montane voles during summer and winter periods in replicate old field and orchard sites. Sample size ($n$ = number of trapping periods) in parentheses.

| | | Replicate 1 | | Replicate 2 | |
|---|---|---|---|---|---|
| Period | | Old field | Orchard | Old field | Orchard |
| Summer 1982 | (7) | 20.4 ± 2.8 | 8.6 ± 1.9 | 10.6 ± 1.7 | 8.1 ± 2.0 |
| Winter 1982-83 | (5) | 20.0 ± 5.4 | 9.2 ± 1.4 | 12.0 ± 2.4 | 7.4 ± 2.8 |
| Summer 1983 | (9) | 17.4 ± 3.3 | 9.9 ± 1.4 | 16.1 ± 2.1 | 8.0 ± 1.3 |
| Winter 1983-84 | (8) | 22.4 ± 4.5 | 10.5 ± 2.1 | 18.4 ± 3.4 | 7.3 ± 1.8 |
| Summer 1984 | (8) | 19.1 ± 3.8 | 2.8 ± 1.4 | 21.0 ± 3.3 | 6.6 ± 1.4 |
| Winter 1984-85 | (6) | 18.5 ± 5.4 | 4.7 ± 1.3 | 17.5 ± 4.8 | 8.7 ± 1.1 |
| Summer 1985 | (9) | 10.9 ± 2.3 | 0.7 ± 0.3 | 8.3 ± 1.5 | 4.1 ± 1.6 |
| Winter 1985-86 | (7) | 8.4 ± 1.4 | 0.3 ± 0.2 | 11.7 ± 2.3 | 1.3 ± 1.0 |

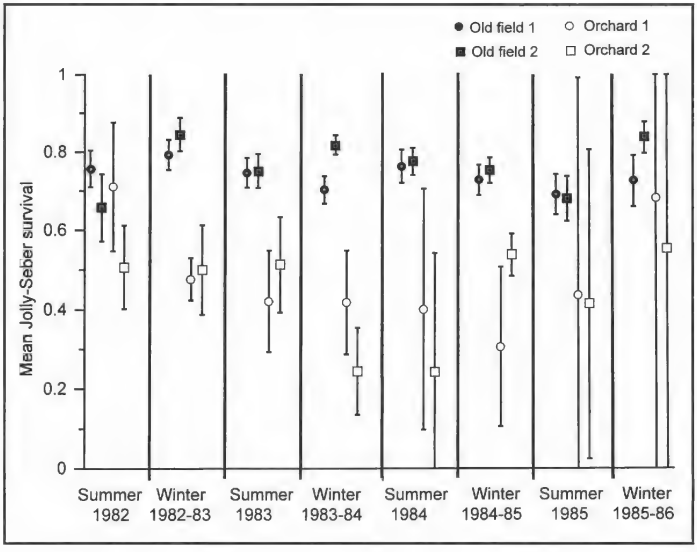


Figure 2. Mean Jolly-Seber survival (per 28 days) ± 95% confidence intervals for montane voles in replicate old field and orchard sites during summer and winter periods in the study.

TABLE 4. Index of early juvenile survival of montane voles (number of juvenile recruits per lactating female) during breeding seasons each year in replicate old field and orchard sites. Sample size (number of lactating females) in parentheses.

| | Replicate 1 | | Replicate 2 | |
|---|---|---|---|---|
| Year | Old field | Orchard | Old field | Orchard |
| 1982 | 2.09 (55) | 4.33 (9) | 2.24 (21) | 2.93 (15) |
| 1983 | 0.81 (175) | 1.45 (44) | 0.60 (164) | 2.85 (20) |
| 1984 | 0.83 (149) | 4.33 (9) | 0.79 (155) | 2.09 (23) |
| 1985 | 0.41 (198) | 2.75 (4) | 0.71 (102) | 1.59 (22) |

Maximum and minimum densities per ha were 186 and 19, which was similar to the range reported for meadow voles by Taitt and Krebs (1985). Conversely, orchard populations had similar mean winter numbers ranging from 29.8 voles/ha in 1982 to 27.8 in 1983 and 25.6 in 1984, before declining to 1.4 in 1985. Thus, montane voles in these orchards appeared to have an annual cycle of abundance with low spring densities and relatively higher numbers in autumn, although the habitat x season interaction was not significant. Old field populations had a multi-annual population fluctuation overlying annual changes in abundance (Figure 1). This dichotomy of population dynamics fits the patterns described for voles for which the amplitude of numerical change is < 5-fold for annual fluctuations and usually >10-fold for multi-annual cycles (Taitt and Krebs 1985).

In the only long-term (19-yr) study, montane vole populations appeared to fluctuate every 3-4 yr at high elevation meadows in Wyoming (Pinter 1986, 1988). This pattern of population fluctuation was similar to the closely related meadow vole (Krebs and Myers 1974, Taitt and Krebs 1985). The temporal heterogeneity inherent in montane habitats for populations of montane voles was also reported by Negus et al. (1977). Negus et al. (1986), however, studied a noncycling population of montane voles over 8 yr in a low elevation salt marsh habitat in Utah.

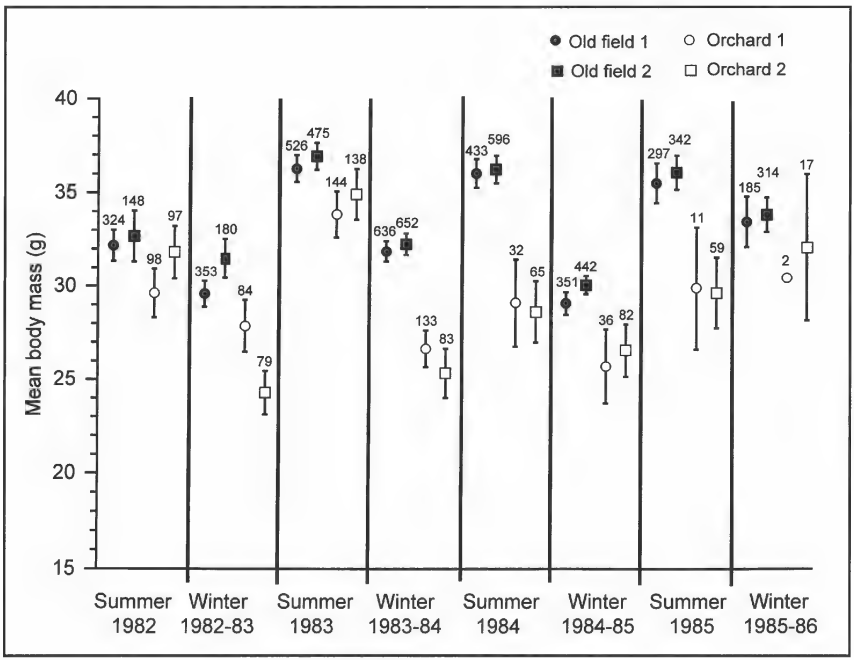


Figure 3. Mean body mass (g) ± 95% confidence intervals for montane voles in replicate old field and orchard sites during summer and winter periods in the study.

Despite the differences in habitat, length of breeding seasons and proportion of reproductive animals were similar in orchard and old field sites. Winter breeding (Jannett 1984) and a long breeding season prior to a peak population of voles are classic characteristics of cyclic behavior and seem to have occurred in these populations. Larger body size at the peak than in other phases of the cycle is another characteristic and may have occurred in the old field sites during summer 1983, winter 1983-84, and summer 1984 (Figure 3). However, mean body mass measurements in summer 1985 and winter 1985-86 did not fit this pattern.

## Orchard Populations

This study is the first intensive mark-recapture analysis of vole populations in orchard agro-ecosystems. Relative population levels of voles have traditionally been monitored by activity measures such as fresh sign or an apple indexing method recording tooth-marks (Byers 1984, 1985). Most vole species require a minimum level of vegetative cover to increase in numbers during multiannual population fluctuations (Birney et al. 1976). Natural grasslands or old fields are the preferred habitats of most *Microtus* spp. (Getz 1985). Thus, it is not surprising that our orchard sites had significantly lower abundance of voles than the old field sites (Table 1). Our orchard sites were mowed, and herbicide was applied to tree rows for weed management, on a regular basis during summer periods. The influence of these cultural practices in reducing vole populations has been reported by Byers and Young (1978), Godfrey (1986), Sullivan and Hogue (1987), and Merwin et al. (1999). Orchard habitats appear to provide a predictable environment for montane voles and thus may explain the relatively consistent, albeit low, abundance patterns over the 4 yr.

We were not able to measure the effect of rodenticides on vole populations as no untreated orchard sites were available for comparison. However, based on the patterns of abundance in the two habitats, orchard population changes may have been influenced more by natural factors than by rodenticides. Merwin et al. (1999) reported that anticoagulant rodenticides did not adequately control meadow voles in apple orchards in New York. Despite the variability in efficacy, rodenticides continue to be the major method used to reduce vole populations in orchards (Byers 1985, Merwin et al. 1999).

The relationship between vole populations in old field or source area habitats and orchards is likely a source-sink whereby lands adjoining an orchard may contribute to population recovery and maintenance through immigrating animals (Horsfall 1964). Clearly, there were substantial populations in our old field sites and during increase periods (e.g. autumn 1983 and 1984), dispersal of voles was high, as documented experimentally by Myers and Krebs (1971) and Krebs et al. (1976). During these periods of high dispersal in autumn and early winter attempts at population reduction are essentially futile owing to the surplus of animals available to colonize depopulated areas (Sullivan 1986). This surplus of animals was particularly dramatic in the outbreaks of montane voles in the western U.S. in 1906-1908 and in 1957-1958 when this microtine caused widespread damage to agricultural crops (Getz 1985).

Orchard populations of montane voles appear to be linked to source area dynamics of populations in old field habitats. Mean abundance of voles/ha ranged from 26.0-125.7 in old field sites and from 0.3-41.4 in orchard sites. Mean recruits/ha also followed this pattern (Table 5). Length of breeding seasons and proportion of reproductive voles were generally similar in old field and orchard sites, but overall survival and mean body mass were consistently higher in old field than

TABLE 5. Summary of the population dynamics of montane voles in old field and orchard habitats over a 4-year period.

| Parameter and period | Old field | Orchard |
|---|---|---|
| Mean abundance per ha (range) | | |
| Summer | 26.0 – 112.4 | 1.2 – 39.3 |
| Winter | 34.9 – 125.7 | 0.3 – 41.4 |
| Mean recruits per ha (range) | | |
| Summer | 8.3 – 21.0 | 0.7 – 9.9 |
| Winter | 8.4 – 22.4 | 0.3 – 10.5 |
| Reproduction (proportion) ($n$=4) | | |
| Males | 0.93 | 0.95 |
| Females | 0.38 | 0.40 |
| Early juvenile survival ($n$=8) | 1.06 | 2.79 |
| Total survival ($n$=8) | | |
| Summer | 0.73 | 0.46 |
| Winter | 0.78 | 0.47 |
| Mean body mass ($n$=8) | | |
| Summer | 35.3 | 31.0 |
| Winter | 31.5 | 27.4 |

orchard sites (Table 5). Traditional methods of vole control (rodenticides) have little effect on vole numbers during peak years as voles from adjacent habitats readily move into orchards. Our study suggests that other methods of vole control (habitat alteration) may be more effective at limiting vole-caused damage.

## Literature Cited


Askham, L. R. 1988. A two year study of the physical and economic impact of voles (*Microtus montanus*) on mixed maturity apple (*Malus* spp.) orchards in the Pacific Northwestern United States. Pages 151-155 *In* A.C. Crabb and R.E. Marsh (editors), Proceedings of the 13th Vertebrate Pest Conference. University of California, Davis, California.

Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto Press, Toronto, Ontario.

Birney, E. C., W. E. Grant, and D. D. Baird. 1976. Importance of vegetative cover to cycles of *Microtus* populations. Ecology 57:1043-1051.

Byers, R. E. 1984. Control and management of vertebrate pests in deciduous orchards of the eastern United States. Horticultural Reviews 6:253-285.

Byers, R. E. 1985. Management and control. Pages 621-646 *In* R. H. Tamarin (editor), Biology of New World *Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, Massachusetts.

Byers, R. E., and R. S. Young. 1978. Effect of orchard culture on pine vole activity. Journal of the American Society for Horticultural Science 103:625-626.

Fisher, A. R., and R. G. Anthony. 1978. The effect of soil texture on distribution of pine voles in Pennsylvania orchards. American Midland Naturalist 104:39-46.

Getz, L. L. 1985. Habitats. Pages 286-309 *In* R. H. Tamarin (editor), Biology of New World *Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, Massachusets.

Godfrey, M. E. R. 1986. Cultural practices affecting montane voles in Washington apple orchards. *In* C. G. J. Richards, and T. Y. Ku (editors), Control of Mammal Pests. Supplement Number 1 to Tropical Pest Management 32: 127-138.

Hilborn, R., J. A. Redfield, and C. J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. Canadian Journal of Zoology 54:1019-1024.

Horsfall, F., Jr. 1964. Pine mouse invasion and reinfestation of orchards subsequent to removal of adjacent woody plant cover or the use of ground sprays. Proceedings of the American Society for Horticultural Science 85:161-171.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Jannett, F. J., Jr. 1984. Reproduction of the montane vole, *Microtus montanus*, in subnivean populations. Pages 215-224 *In* J. F. Merritt. (editor), Winter Ecology of Small Mammals. Carnegie Museum of Natural History Special Publication Number 10.

Jolly, G. M., and J. M. Dickson. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. Canadian Journal of Zoology 61:922-927.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36:239-273.

Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon. Journal of Animal Ecology 55:963-982.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50:587-607.

Krebs, C. J. and J. H. Myers. 1974. Population cycles in small mammals. Advances in Ecological Research 8:267-399.

Krebs, C. J., I. Wingate, J. LeDuc, J. A. Redfield, M. Taitt, and R. Hilborn. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. Canadian Journal of Zoology 54:79-95.

Merwin, I. A., J. A. Ray, and P. D. Curtis. 1999. Orchard groundcover management systems affect meadow vole populations and damage to apple trees. Horticultural Science 34:271-274.

Myers, J. H., and C. J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecological Monographs 41:53-78.

Negus, N. C., P. J. Berger, and J. B. Forslund. 1977. Reproductive strategy of *Microtus montanus*. Journal of Mammalogy 58:347-353.

Negus, N. C., P. J. Berger, and B. W. Brown. 1986. Microtine population dynamics in a predictable environment. Canadian Journal of Zoology 64:785-792.

Pearson, K., and C. G. Forshey. 1978. Effects of pine vole damage on tree vigor and fruit yield in New York orchards. Horticultural Science 13:56-57.

Pinter, A. J. 1986. Population dynamics and litter size of the montane vole, *Microtus montanus*. Canadian Journal of Zoology 64:1487-1490.

Pinter, A. J. 1988. Multiannual fluctuations in precipitation and population dynamics of the montane vole, *Microtus montanus*. Canadian Journal of Zoology 66:2128-2132.



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Reich, L. M. 1981. *Microtus pennsylvanicus*. Mammalian Species 159:1-8.

Seber, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters, 2nd Edition. Charles Griffin, London, UK.

Sullivan, T. P. 1986. Understanding the resiliency of small mammals to population reduction: poison or population dynamics? C. G. J. Richards and T.Y. Ku (editors). *In* Control of Mammal Pests. Supplement Number 1 to Tropical Pest Management 32:69-82.

Sullivan, T. P., and E. J. Hogue. 1987. Influence of orchard floor management on vole and pocket gopher populations and damage in apple orchards. Journal of the American Society for Horticultural Science 112:972-977.

Sullivan, T. P., D. S., Sullivan, and E. J. Hogue. 2000. Impact of orchard vegetation management on small mammal population dynamics and species diversity. Pages 398-403. *In* T. P. Salmon and A. C. Crabb (editors), Proceedings of the 19th Vertebrate Pest Conference, University of California, Davis, California.

Sullivan, T. P., D. S., Sullivan, E. J., Hogue, R. A., Lautenschlager, and R. G. Wagner. 1998. Population dynamics of small mammals in relation to vegetation management in orchard agroecosystems: compensatory responses in abundance and biomass. Crop Protection 17:1-11.

Taitt, M. J., and C. J. Krebs. 1985. Population dynamics and cycles. Pages 567-620 *In* R. H. Tamarin (editor), Biology of New World *Microtus*. Special Publication Number 8. American Society of Mammalogists, Boston, Massachusetts.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

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# Surface Growth Rings of *Porites lutea* Microatolls Accurately Track Their Annual Growth

## Abstract

Microatolls are disk-shaped coral colonies, having perimeters of live coral surrounding dead centers, that are limited in their upward growth by exposure at extreme low tide. We looked at surface annuli of microatolls of *Porites lutea* on the open ocean reef flat of Abaiang Atoll, in the Republic of Kiribati, as potential external indicators of microatoll yearly growth pattern. We measured surface annuli width and disk diameters of 10 microatolls, from March 1998 to October 2000, and found a mean growth rate of 2.2 cm/yr. X-radiography was used to establish a direct connection between surface annuli and internal growth bands. Comparison of the growth pattern of surface annuli to observed monthly mean lower low waters showed that these corals closely track fluctuations in local mean sea level. This suggests that there is a potential for using the surface annuli of *Porites lutea* microatolls on well drained, open ocean reef flats as an ongoing, low cost, non-destructive method of assessing trends in local mean sea level.

## Introduction

Microatolls are disk-shaped shallow water corals that are limited vertically by prolonged subaerial exposure around mean lower low water (MLLW), and constrained to grow only laterally at their circumferences, leaving flat or concave, dead upper surfaces that become covered by sediments, algae, and sessile animals (Figure 1). Water temperature and the duration and intensity of sunlight are important factors limiting photosynthetic activity of zooxanthellae in corals, and thus coral growth, but seasonal fluctuations in water temperature and sunlight on atolls near the equator are not large. On the reef flat, on the other hand, corals experience greater variation in both regimes as a direct consequence of the frequency and level

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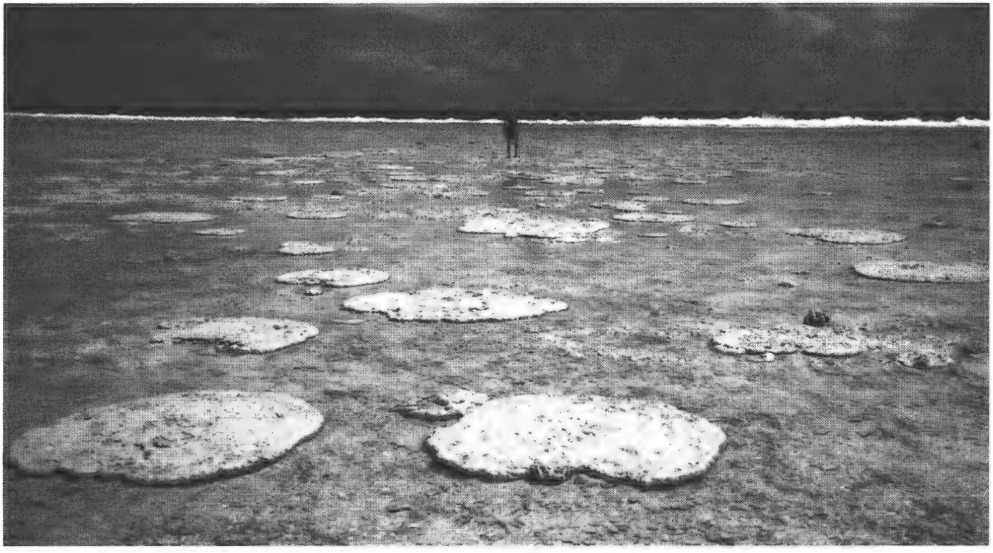

Figure 1. View looking toward reef crest across length of microatoll patch on ocean reef flat, Tabwiroa, Abaiang Atoll, Republic of Kiribati, showing microatolls exposed at low tide.



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of extreme low tides. Temperatures in the shallow waters of the reef flat at low tide increase as the substrate warms, and the filtering effect of seawater against harsh sunlight is lost. Thus, frequency and level of extreme low tides can have important consequences for microatoll growth beyond direct desiccation due to exposure.

Although the formation of microatolls has been discussed in the literature by a number of authors (summarized by Stoddart and Scoffin 1979), little attention had been paid to surface features of microatolls until Woodroffe and McLean (1990) related surface features of microatolls of *Porites* sp. in Kiribati and the Cocos (Keeling) Islands to sea level changes, and (in Kiribati) to the 1982-83 El Niño-Southern Oscillation (ENSO). Spencer et al. (1997) used surface features of *Porites lutea* microatolls on Tongareva Atoll, Northern Cook Islands, to reconstruct sea levels for the previous 57 yr. Smithers and Woodroffe (2000) found that elevation among *Porites* microatolls they surveyed in the Cocos Islands varied more than 40 cm across a range of intertidal environments. Microatolls in open reef flat habitats had the narrowest and most consistent elevation range. They went on to establish chronologies for variations in *Porites* microatoll surface morphology and to correlate these in microatolls from separate reef flat sites in the Cocos Islands (Smithers and Woodroffe 2001).

Of all the different corals that form microatolls, *Porites lutea* is especially interesting to us because it is the only one we have seen that develops distinct and regular concentric rings on the upper surface. We hypothesized that these surface rings (annuli) reflect the annual growth of these microatolls, and proposed a possible link between annulus width on microatolls of *P. lutea* on the island of Mauke, Cook Islands to ENSO frequency (Flora et al. 1996). At that time, however, we did not have the means to test this link adequately.

In 1998, we measured surface annulus widths and corallum diameters of microatolls of *Porites lutea* in the ocean reef flat environment of Abaiang Atoll to determine their rate of growth, and used X-radiography to evaluate the potential connection between surface annuli, internal density bands, and local mean sea level (MSL).

*Porites lutea* has been widely reported to have a high linear annual growth rate, especially in shallow water. Knutson et al. (1972) used auto- and X-radiography to quantify growth rate and density variation in seven species of reef corals on Enewetak Atoll and reported a linear growth rate for *P. lutea* of 1.35 cm/yr. Buddemeier et al. (1974), continuing this line of inquiry, looked at 15 species of corals collected from various depths at Enewetak Atoll and found that growth rate was a function of both species and depth. Their reported annual growth rate for *P. lutea* ranged from 4-5 mm at a depth of 30 m, to 13.5 mm at depths of 3-4 m. Highsmith (1979) studied growth rates in three massive corals, *Favia pallida*, *Goniastrea retiformis*, and *Porites lutea*, also at Enewetak Atoll. Mean linear growth rate for *P. lutea* was only 7.6 mm, but was the highest of the three species. Growth rates for all three declined with depth, being greatest in <5 m of water. Scoffin et al. (1992) studied growth rates in *P. lutea* at sites in South Thailand with different exposures to wave energy, and reported that linear growth rates decreased with increased hydraulic energy. They found that growth rates for *P. lutea* in protected shallows were as high as 2.5 cm/yr.

X-radiography of density bands within the coral skeleton has been widely used for the past 30 yr to assess coral growth rates and environmental factors affecting growth (Knutson et al. 1972, Buddemeier et al. 1974, Weber and White 1977, Highsmith 1979, Barnes and Devereux 1988). It has also been important in evaluating the potential of microatolls to record historical sea levels (Woodroffe and McLean 1990, Spencer et al. 1997, Smithers and Woodroffe 2001). This and other methods, such as auto-radiography and Alizarin staining, are destructive to the reef because they require the collection of all or part of the coral for the analysis. They are also expensive because of the equipment required, and sampling in remote locations like the mid-ocean atolls of Kiribati involves greater logistical problems. We reasoned that if our hypothesis was correct, the widths of surface annuli of *P. lutea* microatolls could be used for ongoing, low-cost, non-intrusive assessment of the coral's growth response to environmental changes on the reef flat, especially to changes in local MSL.

## Methods

The study site is a large oval patch 30 m wide by 100 m long, perpendicular to reef crest and shore,

of ~630 microatolls of *Porites lutea* (Figure 1), located on the windward, open ocean reef flat of Abaiang Atoll, in the Republic of Kiribati. It is ~850 m northwest of the large fish trap outside of St. Joseph's College, in the village of Tabwiroa, and ~125 m out toward the reef crest from the beach (Figure 2). Tides in Kiribati are semidiurnal, with a range of ~2 m and a frequent diurnal inequality of several centimeters. The patch is well drained, and the upper surfaces of microatolls often stand several centimeters above extreme low water (Figure 1).

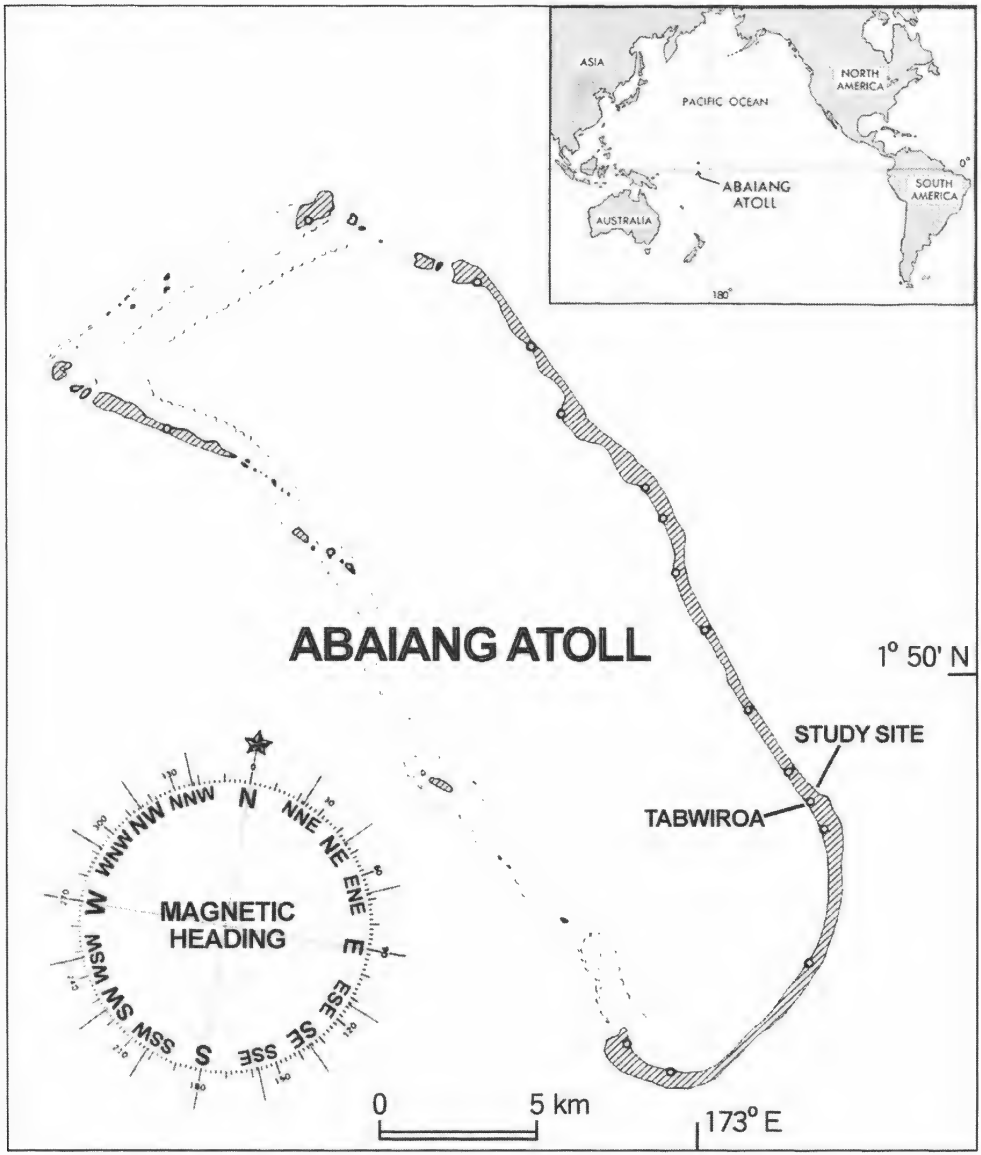



Figure 2. Abaiang Atoll, Republic of Kiribati.

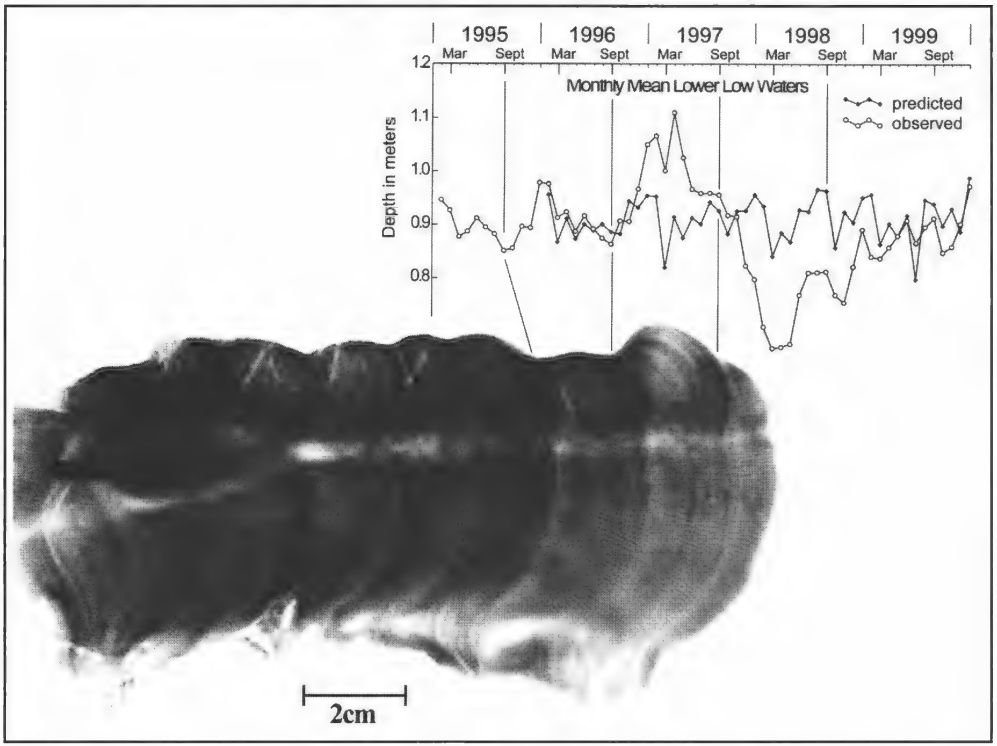



Figure 3. X-radiograph of microatoll #1 vertical cross section, showing internal annual density bands connecting directly with grooves between surface annuli. The outside edge of the microatoll is on the right. Graph compares surface annuli with observed and predicted MLLW for the period 1996-1999.

We identified this coral to species through microscopic examination of calicular features given by Veron (1986), and comparison with other known species of *Porites*. Most important characters were a fused triplet, five palli, and five radii.

Two methods were used to assess growth rate of *Porites lutea* microatolls. The first method measured surface annuli. The boundaries between surface annuli in *P. lutea* microatolls are represented by grooves in the microatoll surface corresponding to periods of retarded or arrested growth of the coral skeleton (Figures 3, 4). However, build-up of coralline algae, and the effects of mechanical and bio-erosion can obscure grooves between annuli, especially toward the microatoll center. Thus, the newest annuli, at the perimeter, are most distinct, while those toward the center become less distinct. Most microatolls in this study contained 9-10 annuli clear enough to be reliable. Mean annual growth rate was calculated on the measurement of these clear annuli.

In March and April, 1998, 10 microatolls in the patch, 40–100 cm in diameter, were chosen for the clarity of their surface annuli (i.e., a minimum of breakage, erosion, or excessive overgrowth by coralline algae). The upper surfaces of the microatolls were cleaned of sediment and fleshy algae to reveal their annulations more clearly. Of the 10 microatolls, 9 were sketched, and all 10 were photographed, at the time of measurement. Their locations were recorded, based on their distance and magnetic compass bearing from each other and from the beach. Three transects, separated by as much as 45°, were measured across the top of each microatoll. The direction of each transect was recorded as the compass bearing the investigator faced, (90° to the line of the transect itself) while recording transect measurements. A

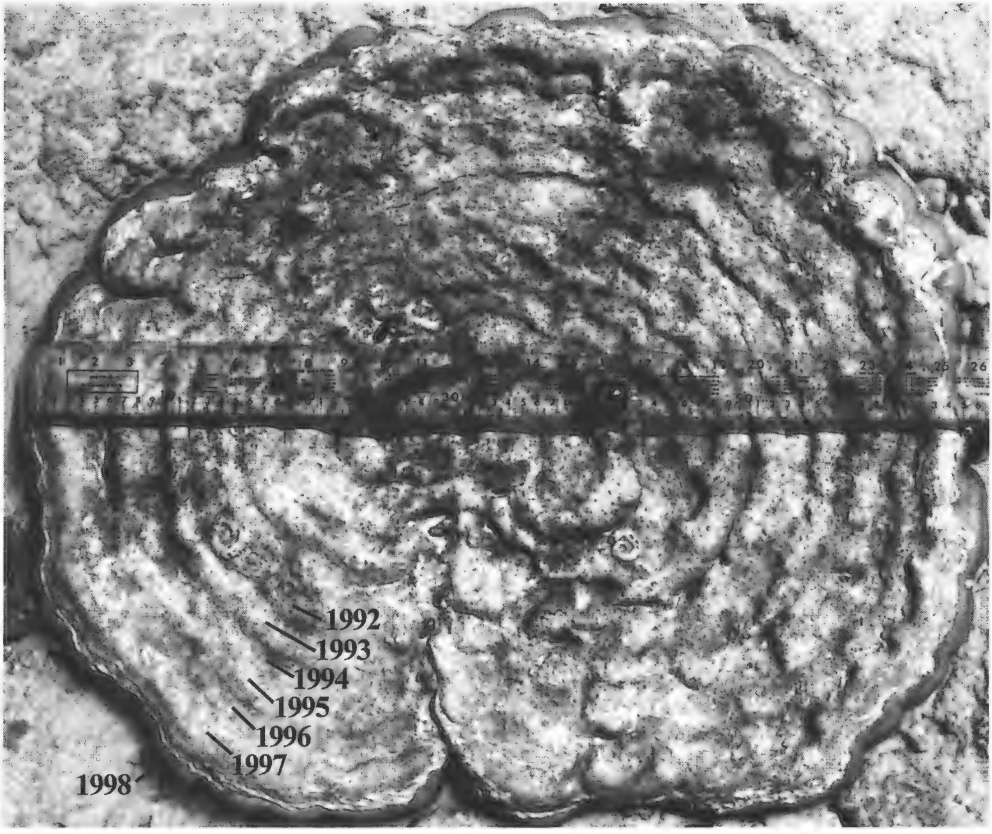



Figure 4. Transect measurement of a cleaned microatoll (Microatoll #3).

meter stick was laid across the full diameter of the microatoll, excluding live coral tissues at the perimeter, and passing as closely as possible through its estimated center (Figure 4). The maximum diameter was read as the distance from the interface between live coral tissues and dead coral skeleton on one side, to the same interface on the opposite side. The width of each growth band, or annulus, was measured from groove to groove, starting from the outside edge at either end of each transect, and working toward the center insofar as the annuli remained distinct enough to read with reasonable certainty. Thus each transect gave two radii, recorded as left and right for each transect number, for a total of six radii per microatoll.

The growth pattern of a single microatoll can vary from one spot to another only centimeters apart, making evaluations based upon only a few measurements unreliable. We averaged all measurements, across all transects, from 10 microatolls to arrive at the mean values for each individual annulus reported in Table 1. This allowed us to project an archetypal or representative microatoll.

TABLE 1. Mean annulus widths (cm) of *Porites lutea* microatolls by deposition year. Means with the same superscripted letters are not significantly different.

| Deposition year | 1997 | 1990 | 1989 | 1991 | 1995 | 1992 | 1988 | 1993 | 1994 | 1996 |
|---|---|---|---|---|---|---|---|---|---|---|
| Mean annulus width | 2.75 | 2.37[a] | 2.32[ab] | 2.21[ab] | 2.17[ab] | 2.02[ab] | 2.0[abc] | 1.97[bc] | 1.70[cd] | 1.64[cd] |

TABLE 2. Annual growth rate of *Porites lutea* microatolls by measurement of increase in diameter over 30 mo from March, 1998 to October, 2000.

| Microatoll number | Mean radius increase (cm) | Mean radius increase (cm) per day | Mean radius increase (cm) per year |
|---|---|---|---|
| 2 | 4.90 | 0.0052 | 1.90 |
| 3 | 5.30 | 0.0058 | 2.12 |
| 4 | 5.80 | 0.0065 | 2.39 |
| 5 | 5.55 | 0.0061 | 2.23 |
| 6 | 6.35 | 0.0070 | 2.54 |
| 7 | 4.65 | 0.0051 | 1.88 |
| 8 | 6.10 | 0.0068 | 2.48 |
| 9 | 5.85 | 0.0065 | 2.38 |
| 10 | 5.30 | 0.0059 | 2.16 |

By this method, we evaluated both intra-annual and inter-annual growth patterns with greater confidence.

The second method assessed growth rate of *Porites lutea* microatolls by measuring the increase in outside diameter of microatolls over time. In September and October, 2000, these same transects, except those of #1, were measured again to determine the increase in diameters of the nine microatolls over the intervening 30 mo. The number of days between measurements in 1998 and 2000 varied among microatolls and were used accordingly to calculate mean radius increase in cm/yr for each microatoll (Table 2). These values were then used to arrive at an overall mean annual growth rate for *P. lutea*. The distinctly wider and more vertically prominent 1997 annulus was used as a marker for visually assessing the increase in the number of annuli during this time period (Figure 5).

The possible correlation between surface annuli and internal growth bands within the coral skeleton was assessed on microatoll #1. A vertical slab of the coral, 1.3 cm wide, was cut parallel to the growth axis, from circumference to center, and an X-ray exposure was made using a Benett 100/300 radiographic unit on 800 speed ImageTek-B film at 50 kv for 4/10 of a second.

We compared the pattern of annulus growth in the photographs taken in 2000 and the X-ray image of microatoll #1 to plots of predicted monthly MLLW for 1996–1999 and observed monthly MLLW for 1995–1999 (Figure 3). These predicted and observed levels of monthly MLLW were derived from hourly MSL data provided by the National Tidal Facility (NTF) at Flinders University of South Australia from their KIR1 tide gauge at Betio, Tarawa. The NTF was not producing official tidal predictions for Kiribati prior to 1997, but kindly generated residuals (observations minus predictions) for us using their 2003 basis for predictions.

## Results

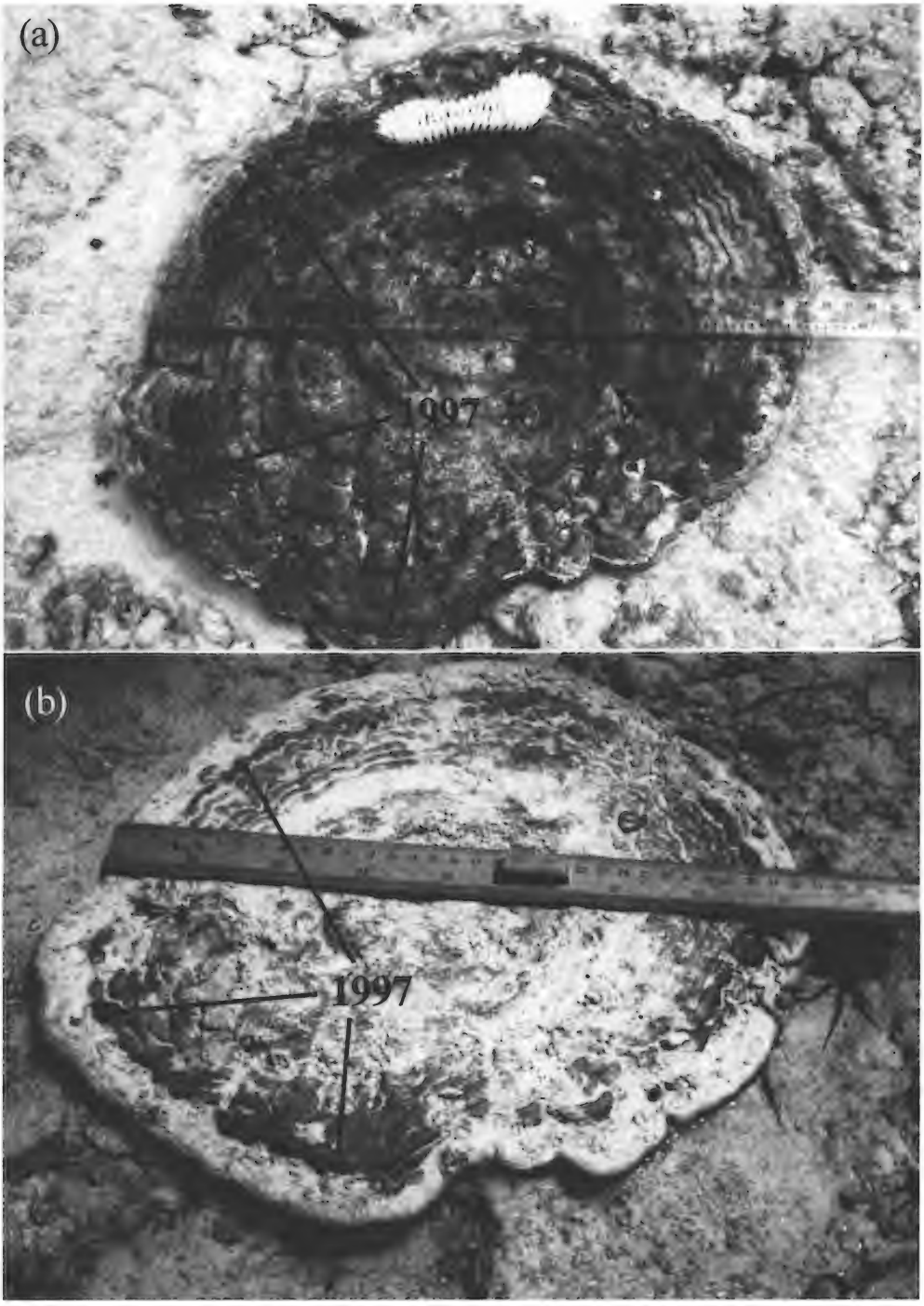
Overall mean growth rate estimated by measuring annulus width was 2.12 ± 0.10 cm/yr, compared to 2.23 ± 0.08 cm/yr for diameter increase. Both methods produced similar results, with a difference of merely 0.11cm.

The 1997 annuli were significantly wider ($P$=0.05) than any other year, based on ANOVA and multiple range tests (Table 1). These annuli were the widest and most vertically prominent of the 10 annuli measured (Figure 5). At the low end of the scale, the differences among 1988, 1993, 1994, and 1996 were not significant. However, 1993 and 1988 were part of a continuum of non-significant differences that extended through the remaining years (Table 1), which confuses the overall relationships. Generally, these other years varied slightly around the overall mean (2.04), whereas the ENSO year (1997) was clearly wider.

Annual growth data measured over 30 mo on 9 microatolls were remarkably similar. Mean radius increase during the study ranged from 4.9 to 6.4 cm, and mean daily radius increase ranged from 0.0051 to 0.0070 cm/day (Table 2).

X-radiography of the cross section of microatoll #1 confirmed a direct relation between surface annuli and internal growth bands in the skeletal matrix (Figure 3). The curve of the convex upper surface of each annulus continues into the matrix of the coral skeleton as a distinctly denser band in the growth pattern. The arrested growth represented by this high density portion of the skeleton seems to occur around September each year during our sample period. We based this assumption

Figure 5. *(Opposite)* Microatoll growth over 30 mo. (a) photograph of Microatoll #7 taken in April 1998. The 1997 annulus is the first annulus inside live growth at the perimeter. (b) photograph of Microatoll #7 taken in October 2000. The 1997 annulus is well inside (>5 cm) live growth at the perimeter representing the year 2000, with two new annuli (1998 and 1999) between.


(a)
1997
(b)
1997

on the relative distance between the growing edge (collected in March) and the first high density band, compared to that between the first and second high density bands bracketing the 1997 annulus.

There was a marked difference between predicted and observed tidal levels for 1997 and 1998 acquired from NTF data (Figure 3). Observed MLLW values for 1997 were approximately 15 cm higher than predicted values, while observed values for 1998 were roughly the same magnitude below predicted values. This discrepancy was reflected in the growth patterns observed in *Porites lutea* microatoll annuli for the same period.

## Discussion

Our reported growth rate of 2.2 cm/yr for *Porites lutea* at <2 m depth is consistent with growth rates, ranging up to 2.5cm/yr, arrived at by earlier investigators for this species in shallow water. The increase over time that we measured in microatoll diameter and concomitant increase in number (2) of surface annuli (Figure 5), together with the direct connection we found between surface annuli and internal growth bands through X-radiography (Figure 3), confirmed our hypothesis that surface annuli accurately reflect annual growth in this coral.

The height of the 1998 annulus was sub-normal, while the 1999 annulus was approximately the same level as those previous to 1997 (Figure 5). This constraint of the 1998 growth is similar to that reported by Woodroffe and McLean (1990), who associated a 1983 hiatus in the growth pattern of *Porites* microatolls on Abemama with the 1982-83 ENSO. However, they reported no increase in *Porites* growth in 1982, while the increase we observed in 1997 was marked. They reported only a slight increase in local MSL in 1982, followed by a drop of about 15 cm in 1983. The increase we observed in *P. lutea* microatoll growth in 1997 and subsequent hiatus in 1998 is comparable to the rise and fall in observed monthly MLLW for Kiribati during that same period (Figure 3).

Normal annual tidal fluctuations can be seen in the regular growth pattern of surface annuli in reef flat *Porites lutea* microatolls. However, normal tidal levels on the reef flat may be augmented during the early part of a strong ENSO event when surface waters, normally stacked up in the equatorial western Pacific by strong trade winds, flow eastward when the trade winds are disrupted under ENSO conditions. Abaiang Atoll experienced strong westerly winds during the 1997 ENSO, and some villages sustained flood damage due to higher than normal waves coming across the lagoon from the west. These unusual effects on the tide are reflected in Figure 3 in the comparison between predicted MLLW for 1996-1999 and observed MLLW for the same period. The anomalous tidal levels during the 1997-98 ENSO were not forecast in the normal tidal predictions because they were caused by different phenomena, but they show up clearly in the observed MLLW, which are based on hourly sea level measurements.

Our findings corroborate those of Woodroffe and McLean (1990) and Spencer et al. (1997), and demonstrate that the growth patterns in the upper surface of the *Porites lutea* microatolls we studied on Abaiang Atoll closely reflect variations in local MSL. Furthermore, while previous research has required X-radiography and other destructive means to elucidate historical data, we have shown that surface annuli of *P. lutea* microatolls can be used to track ongoing variations visually, without damage to the corals, and with a minimum of equipment. Thus, with sufficient replication to ensure a statistically meaningful sample size, the surface annuli of *P. lutea* microatolls in the open ocean reef flat of mid-Pacific atolls could be measured annually for an ongoing, low-cost, non-intrusive assessment of the coral's response to fluctuations in local MSL. As inner annuli become less distinct and drop out of the record, the newest outer annuli are added, maintaining a consistent, but dynamic data base of about 10 annuli each year. Cumulatively, these data would represent an important adjunct to tide gauge records and, where tide gauges are not available, a significant record in their own right.

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## Literature Cited


Barnes, D. J., and M. J. Devereux. 1988. Variations in skeletal architecture associated with density banding in the hard coral *Porites*. Journal of Experimental Marine Biology and Ecology 121:37-54.

Buddemeier, R. W., J. E. Maragos, and D. W. Knutson. 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. Journal of Experimental Marine Biology and Ecology 14:179-200.

Flora, C. J., R. Flora, P. Ely, and E. C. Parish. 1996. Ringed coral disks on Mauke in the Cook Islands and El Niño frequency. Page 63 *In* H. A. Lessios (editor), 8th International Coral Reef Symposium Abstracts, Panama City, Panama.

Highsmith, R. C. 1979. Coral growth rates and environmental control of density banding. Journal of Experimental Marine Biology and Ecology 37:105-125.

Knutson, D. W., R. W. Buddemeier, and S. V. Smith. 1972. Coral chronometers: seasonal growth bands in reef corals. Science 177:270-272.

Scoffin, T. P., A. W. Tudhope, B. E. Brown, H. Chansang, and R. F. Cheeney. 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. Coral Reefs 11:1-11.

Smithers, S. G., and C. D. Woodroffe. 2000. Microatolls as sea-level indicators on a mid-ocean atoll. Marine Geology 168:61-78.

Smithers, S. G., and C. D. Woodroffe. 2001. Coral microatolls and 20th century sea level in the eastern Indian Ocean. Earth and Planetary Science Letters 191:173-184.

Spencer, T., A. W. Tudhope, J. R. French, T. P. Scoffin, A. Utanga. 1997. Reconstructing sea level change from coral microatolls, Tongareva (Penrhyn) Atoll, Northern Cook Islands. 8th International Coral Reef Symposium, Panama 1:489-494.

Stoddart, D. R., and T. P. Scoffin. 1979. Microatolls: review of form, origin, and terminology. Atoll Research Bulletin 224:1-17.

Veron, J. E. N. 1986. Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu, Hawaii.

Weber, J. N., and E. W. White. 1977. Caribbean reef corals *Montastrea annularis* and *Montastrea cavernosa*: long-term growth data as determined by skeletal X-radiography. Reefs and related carbonates - ecology and sedimentology. American Association of Petroleum Geologists, Tulsa, Oklahoma.

Woodroffe, C., and R. McLean. 1990. Microatolls and recent sea level change on coral atolls. Nature 344:531-534.



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# A Time Comparison Study of Vegetation on The Island Research Natural Area in Central Oregon

## Abstract

This study on The Island, a Research Natural Area (IRNA) in the central Oregon western juniper zone, measured vegetation cover during the early 1990s and compared it to an earlier study conducted in the early 1960s. Two plant associations were studied: western juniper/big sagebrush/bluebunch wheatgrass and western juniper/bitterbrush/bluebunch wheatgrass. The same study design and measurement techniques were used in both studies to document percent cover of vegetation on study-site macroplots, microplots, and aerial photographs. Major differences noted by 1993 included greater juniper and shrub cover, primarily big sagebrush, a more even mix of grass species rather than a dominance of bluebunch wheatgrass and cheatgrass as noted in the 1960 study, and higher litter cover. Weather data from 1952-1993 were analyzed, and no major events or trends were found in the 30 yr period between studies. This study also compared present-day IRNA sites in both plant associations with sites located in the nearby grasslands that had experienced greater impact from livestock and humans. The comparison sites had higher tree and shrub cover than IRNA and differed in Idaho fescue and bluebunch wheatgrass cover. Finally our study was compared to another recent study in the western juniper/big sagebrush/bluebunch wheatgrass plant association on IRNA. We established new representative macroplots whereas the other study used the exact plots of the 1960s study. Results were similar showing that either method may be satisfactory. A continuing bank of data sets of vegetation change and land use will assist us to understand the complexities of plant community dynamics over time.

## Introduction

To study ecosystem dynamics and successional change it is absolutely necessary to develop long-term data sets on plant community populations (Franklin and Dyrness 1988). The Island Research Natural Area (IRNA) in the central Oregon western juniper (*Juniperus occidentalis*) zone provides an opportunity to study vegetation change in the relative absence of human impact or recent natural disturbance. It is a unique, semi-relict mesa located southwest of Madras (Figure 1). IRNA was first studied in the early 1960s by Driscoll (1962, 1964a, 1964b). Because of its isolated location it has avoided the fate of much of this area which Barbour et al. (1999) describes as having been converted to farmland or historically overgrazed and now invaded by weedy annuals and short-lived perennials.

Opportunities to build on past data sets are few, especially in plant communities that remain relatively undisturbed. Long-term studies reported in the literature on similar habitats include rangeland in southeastern Idaho (Anderson and Holte 1981), sagebrush grassland in eastern Oregon (Sneva et al. 1984), sagebrush semi-desert in west central Utah (West et al.1984), and the Horse Ridge Research Natural Area in central Oregon (Knapp and Soulé 1998). These studies were on sites with various intensities and frequencies of human and natural disturbance.

Once field studies are completed, causal factors of vegetation change are particularly difficult to evaluate. Mechanisms driving succession have been debated for nearly a century, and the debate is likely to continue into the future (Barbour et al. 1999). Disturbance regimes in the arid and semiarid western USA are complex and impacted by a mixture of anthropogenic and natural events (Hobbs and Huenneke 1992).

Without disturbance, especially without fire, a tree/shrub/grass plant community will develop slowly toward a dominance of woody vegetation (West et al 1984). Without periodic fire, big sagebrush (*Artemisia tridentata*) and juniper may outcompete perennial grasses through more efficient use of water, nutrients, and space (West et al.1979, Eddleman and Miller 1992). More shrub cover and less grass cover may also be caused by big

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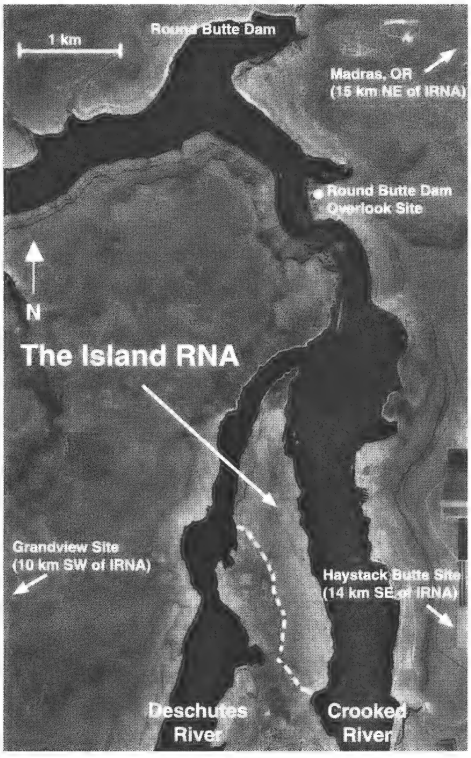


Figure 1. Digital orthophoto map of the study area (from Round Butte Dam, OR quadrangle)

sagebrush with its longer growing period outcompeting grasses for soil moisture, nitrogen, and other nutrients (Hyder and Sneva 1956, Doescher et al. 1984, Miller et al. 1986). Rooting structure plays a role in competition. Two dominant shrubs found in the juniper zone are bitterbrush (*Purshia tridentata)* and sagebrush. Bitterbrush requires stony soils with discontinuous hardpan and cracked bedrock, confining it to certain areas. Big sagebrush with a 1-4 m stout taproot and wide spreading lateral roots is more competitive and widespread (Frischknecht 1963).

Differences in life history traits and their interacting with environmental change are a crucial mechanisms driving succession (Barbour et al. 1999). Livestock grazing and human impact on a site results in higher tree and shrub cover and lower grass cover (Madany and West 1983). Invasive alien species may be brought to a site by livestock and humans. Grasses such as cheatgrass (*Bromus tectorum*), medusahead (*Elymus caput-medusae*), and red brome (*Bromus rubens*) are of concern in the western juniper zone. Medusahead is extremely competitive crowding out native grasses and the alien, cheatgrass (Whitson 1991).

The purpose of this study was twofold. First we measured the present vegetation on IRNA to compare our data with other studies. Driscoll (1962, 1964a, 1964b) documented two plant communities on IRNA: juniper/sagebrush/wheatgrass and juniper/bitterbrush/wheatgrass. A later study of the juniper/sagebrush/wheatgrass plant association located the plots of this earlier study and remeasured vegetation cover (Knapp and Soulé 1996). We established new plots in 1992 and 1993 in both plant associations and collected percent cover data for shrubs, grasses, forbs, and ground cover. We also examined change in western juniper cover over a 50-yr time period using aerial photos available for each decade back to the mid 1940s.

The second part of our study compared present-day vegetation cover on IRNA with sites in the two established plant associations, but located off the IRNA mesa in accessible areas with land use histories more impacted by humans and livestock than IRNA. These comparison sites were chosen because native species still dominated and few invasive or introduced species were present. They also had similar edaphic and climatic conditions.

## Study Area

IRNA is located immediately south of the confluence of the Deschutes and Crooked Rivers east of the central Oregon Cascades (Figure 1). While known as The Island, it is technically an isolated plateau on the tip of a peninsula. This plateau is 730 m in elevation, and when first studied in 1960 and 1961 was surrounded by steep cliffs up to 200 m (Driscoll 1962, 1964a & b). In 1964 Round Butte Dam was completed, and the Crooked River and Deschutes River canyons were partially filled to form Lake Billy Chinook. Today the cliffs surrounding IRNA average 137 m in height above the surface of the water (Orr and Orr 1999). Access to the site is limited to a primitive trail winding up the cliffs near the south end of the peninsula. IRNA is a part of the Deschutes-Columbia Plateau formed by a lava flow approximately one million years ago (Orr and Orr 1999). The area around IRNA beyond the river canyons is gener-

ally a flat mosaic of farmland, pasture, and open rangeland, 730-884 m elevation, with occasional buttes rising to 1220 m. Our three comparison sites are in this open rangeland within 15 km of IRNA.

Weather records from the Metolius Station, northeast of IRNA, depict a semi-arid climate. Summers have warm days and cool nights, and winters are cool to cold. Average annual precipitation is 259 mm and annual mean temperature is 8.7°C (Oregon Climate Service 2002).

Vegetation in the study areas is classified in the western juniper zone, which lies in a savanna between ponderosa pine (*Pinus ponderosa*) forests and the shrub-steppe (Franklin and Dyrness 1988). Woody vegetation consists primarily of scattered western juniper, widely distributed big sagebrush, and narrowly distributed bitterbrush. Characteristic native perennial grasses are bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), Thurber's needlegrass (*Stipa thurberiana*), and Sandberg's bluegrass (*Poa sandbergii*). Annual grasses include slender fescue (*Festuca octoflora*) and the alien cheatgrass. Botanical nomenclature follows Hitchcock and Cronquist (1973).

Soils on the IRNA are classified as an Agency-Madras complex (USDA Natural Resources Conservation Service 2002). Two soil series were described for the juniper/sagebrush/wheatgrass association, covering ~87 ha. Both were nonstony, brown loams, one was 66 cm deep, the other 33 cm deep. Both series contained a clay layer from 20-38 cm deep (Driscoll 1964a). A single soil series was described for the juniper/bitterbrush/wheatgrass plant association, occupying ~14 ha. It was a shallow, sandy loam Regosol overlying a stony clay loam with high stone content. A discontinuous hardpan and cracked bedrock allowed some deep root penetration (Driscoll 1964a).

The first of three comparison sites was the Round Butte Dam Overlook site located 2 km south of the dam overlook building on the east side of Lake Billy Chinook and 5 km northeast of IRNA. The second site was on top of Haystack Butte, 14 km southeast of IRNA on the east side of US Highway 97. Both sites are in the juniper/sagebrush/wheatgrass plant association. The third site, Grandview, was located 10 km southwest of IRNA just north of the Grandview Cemetery. This site represents the juniper/bitterbrush/wheatgrass association. Soils on two of the comparison sites, Round Butte Dam Overlook and Grandview, are similar to those of IRNA and in the Agency-Madras complex. Soils on the Haystack Butte site are in the Tub series which is 100 cm deep with loam overlying clay loam and cobbly clay at 60 cm (USDA Natural Resources Conservation Service 2002).

## Methods

During the summers of 1992 and 1993 we measured shrub, grass, forb, and ground cover using the same macroplot layout and measurement methods as used by Driscoll (1964a) and earlier described by Poulton and Tisdale (1961). We were unable to relocate Driscoll's exact macroplots, although the two plant associations were easily relocated, and new macroplots were randomly located in representative stands in each.

Fourteen 15x30 m macroplots were established, seven in each of the two associations with locations recorded using GPS equipment (Fox 1995). We avoided ecotones and scabland areas near the western rim and also omitted mature juniper trees within macroplots, as in the earlier study (Richard S. Driscoll, USDA Forest Service retired, Boulder, Colorado, personal communication). Four 1x15 m belt transects were placed within each macroplot. Line transects ran parallel along the belt transects with ten 30x60 cm microplots evenly spaced along each line transect (Figure 2).

Within each microplot percent foliage cover was estimated to the nearest 10% for all herbaceous species, bare ground (including rock), and litter (including moss and lichen). Shrub cover was measured by recording the distance to the nearest 1 cm bisected by each shrub species along the line transect. Shrub height and canopy diameter were measured for all shrubs rooted within the meter wide belt transect.

Macroplots in the juniper/sagebrush/wheatgrass association were located in the central and southern area of IRNA. Macroplots in the juniper/bitterbrush/wheatgrass association were located near the eastern edge of IRNA and labeled juniper/bitterbrush/wheatgrass East. We were also interested in scattered small areas where the juniper/bitterbrush/wheatgrass association occurred, which Driscoll (1964a) did not mention. Macroplots were established in three such areas and are labeled juniper/bitterbrush/wheatgrass South and West.

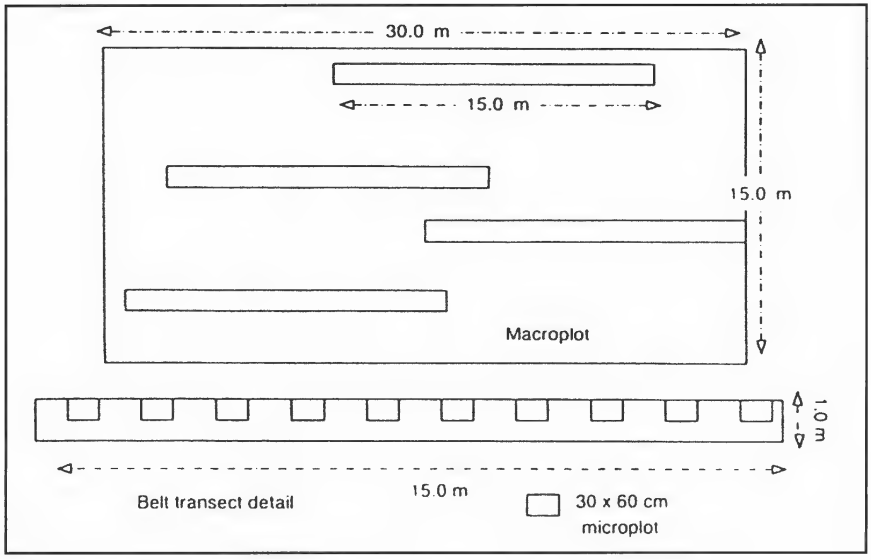


Figure 2. Macroplot, microplot, and belt transect layout

Two macroplots were established at each of the three comparison study sites off the IRNA plateau.

Aerial photographs were used to determine tree cover of western juniper on IRNA and the comparison sites at six time intervals over a 51 yr period: 1944, 1951, 1961, 1975, 1985, and 1995. Enlarged grayscale photocopies were made of aerial photos, and a plastic line/dot grid was placed over the sites to estimate percent cover of the visible juniper trees within each association, a method described by Moessner (1960) and used by Driscoll (1964a).

Weather data from 1952-1993 collected at the Metolius Station, 9 km northeast of IRNA, were examined for climatic trends using regression analysis. Available temperature data used for this study included mean annual, mean monthly maximums and minimums, and monthly extremes. Annual precipitation was examined as was monthly data for the two decades surrounding the 1960s and 1990s studies (Figures 3, 4).

Percent cover results for our plots on IRNA were compared with other studies (Driscoll 1964a,

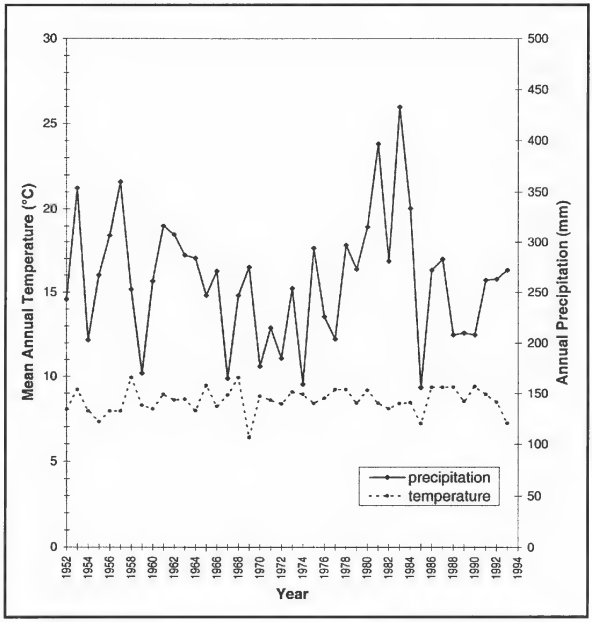


Figure 3. Mean annual temperature and precipitation (Metolius Station) 1952–1993

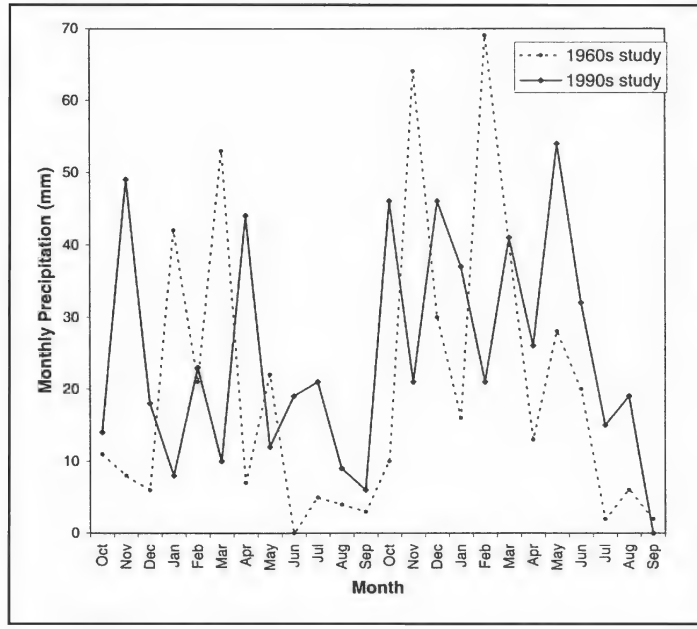


Figure 4. Monthly precipitation (Metolius Station) during the 1960s and 1990s studies

Knapp and Soulé 1996) and with our plots off IRNA for statistically significant differences using Student's t-test. Driscoll reported standard error for some species but not others. When he did not report a standard error, we used our standard error adjusted to his sample size as his reported standard errors were similar to ours.

## Results

Temperature patterns recorded at the Metolius Station were fairly consistent from 1952 to 1993. While the annual mean temperature was 8.7° C and varied little from year to year there were variations between a July mean of 18.2° C and a January mean of 0.05° C. July mean maximum temperature was 29° C and January mean minimum was -4.9° C.

Annual precipitation was highly variable. Years above and below the long term mean of 259 mm were intermittent. Annual precipitation extremes ranged from a high of 397 mm in 1981 to a low of 156 mm in 1985. Three additional years were recorded above 320 mm and three below 200 mm, but no particular pattern emerged from the fluctuations scattered over the recorded 41 yr period (Figure 3). Monthly precipitation patterns varied markedly. The month in which the highest precipitation occurred included every month of the year. A comparison of monthly precipitation for two decades surrounding the study years, 1954-1963 and 1984-1993, found only May was significantly higher in the earlier decade (Figure 4).

Woody vegetation cover in the juniper/sagebrush/wheatgrass association consisted of one tree species, juniper, scattered unevenly throughout the association and one dominant shrub, sagebrush. Grass cover was divided evenly between four native perennial bunchgrasses. The two annual grass species played only a minor role. It is notable that shrub cover was slightly higher than grass cover (Table 1).

The juniper/bitterbrush/wheatgrass East plots consisted of juniper and a mix of two shrubs. Bitterbrush was the dominant shrub, but sagebrush was also present. The grass cover was a fairly even mix of four native perennial grasses plus the alien annual cheatgrass. In this association grass cover was higher than shrub cover. The juniper/bitterbrush/wheatgrass South and West plots varied from the East plots with more sagebrush

and less bitterbrush present. The grass cover was lower than on the East plots. The four native perennials and two annuals were present, but bluebunch wheatgrass and Sandberg's bluegrass dominated (Table 2).

TABLE 1. Mean percent cover for the IRNA juniper/sagebrush/wheatgrass plant association. Values followed by different letters indicate significant differences ($P \leq 0.05$). 1960s data from Driscoll (1964a)

| Species | 1960s study | 1990s study |
|---|---|---|
| Juniper | 10.0[a] | 10.5[a] |
| Sagebrush | 8.5[a] | 15.4[a] |
| Bitterbrush | 0.0 | 0.0 |
| Other shrubs | 1.1 | tr. |
| Total Shrub | 9.6[a] | 15.4[a] |
| Thurber's needlegrass | 2.0[a] | 2.9[a] |
| Bluebunch wheatgrass | 9.2[a] | 3.4[b] |
| Idaho Fescue | 0.4[a] | 2.6[a] |
| Sandberg's bluegrass | 1.3[a] | 2.8[b] |
| Cheatgrass | 1.7[a] | 0.1[b] |
| Slender fescue | 0.6[a] | 0.4[a] |
| Total Grass | 15.2[a] | 12.2[b] |
| Bareground/rock | 41.3[a] | 35.3[a] |
| Litter/moss/lichen | 30.7[a] | 55.9[b] |

TABLE 2. Mean percent cover for the IRNA juniper/bitterbrush/wheatgrass plant association. Values followed by different letters indicate significant differences ($P \leq 0.05$). 1960s data from Driscoll (1964a).

| | | 1990s study | |
|---|---|---|---|
| Species | 1960s study | East plots | South & West plots |
| Juniper | 4.0[a] | 8.7[a] | 10.0 |
| Sagebrush | 0.0[a] | 2.1[a] | 8.2 |
| Bitterbrush | 8.7[a] | 9.8[a] | 5.3 |
| Other shrubs | 0.6[a] | 1.2[a] | tr |
| Total Shrub | 9.3[a] | 13.1[a] | 13.5 |
| Thurber's needlegrass | 1.1[a] | 4.6[b] | 0.4 |
| Bluebunch wheatgrass | 6.2[a] | 2.5[b] | 5.3 |
| Idaho fescue | 0.5[a] | 4.8[b] | 0.6 |
| Sandberg's bluegrass | 0.4[a] | 3.9[b] | 2.9 |
| Cheatgrass | 12.4[a] | 2.6[b] | 0.3 |
| Slender fescue | 0.3[a] | 0.6[a] | 1.1 |
| Total Grass | 20.9[a] | 19.0[a] | 10.6 |
| Bareground/rock | 18.7[a] | 22.2[b] | 33.5 |
| Litter/moss/lichen | 62.3[a] | 57.5[a] | 52.2 |

Forbs were not abundant in IRNA in either plant association. Our study showed < 1% cover. We recorded 14 forb species present in the microplots and identified more than 40 species of forbs in the two associations (Fox 1995).

Open space between the shrubs, grasses, and forbs accounted for a high percent of total cover. The two plant associations showed similar results of > 30% bare ground and > 50% litter cover (Tables 1, 2).

Juniper cover increased gradually but steadily from 1944 to 1995 in both associations on IRNA. The percent cover differences were small when comparing one decade to the next, but significantly more cover was found in 1995 than in 1944. Tree cover on the juniper/sagebrush/wheatgrass sites was only slightly higher than on the juniper/bitterbrush/wheatgrass sites (Table 3).

TABLE 3. Mean percent cover for western juniper on IRNA by plant association. 1961–62 data from Driscoll (1964a); photo date not specified by author

| Year | Juniper/ sagebrush/ wheatgrass | Juniper/ bitterbrush/ wheatgrass East | Juniper/ bitterbrush/ wheatgrass South & West |
|---|---|---|---|
| 1944 | 5.5 | 4.4 | 4.7 |
| 1951 | 8.0 | 4.4 | 5.7 |
| 1961–62 | 10.0 | 4.0 | |
| 1961 | 8.6 | 5.8 | 5.8 |
| 1975 | 8.2 | 5.2 | 6.1 |
| 1985 | 10.1 | 7.5 | 8.9 |
| 1995 | 10.5 | 8.7 | 10.0 |

All of the less pristine, comparison sites off IRNA had somewhat higher juniper and shrub cover than found on IRNA. Juniper cover was significantly higher on the Grandview and Haystack Butte sites. Bitterbrush cover was significantly higher on the Grandview site compared to the juniper/bitterbrush/wheatgrass association on IRNA (Table 4).

Grass components on the comparison sites differed significantly from IRNA. On the Round Butte Dam Overlook site Idaho fescue cover was lower. On the Haystack Butte site Thurber's needlegrass and bluebunch wheatgrass cover were lower but Idaho fescue higher. On the Grandview site the grass mix was similar to IRNA except that Idaho fescue was absent. Only the Grandview site had significantly higher levels of bare ground

TABLE 4. Mean percent cover for the 1990s study of the IRNA and nearby comparison plots. Values followed by different letters indicate significant differences ($P \leq 0.05$).

| Species | Bitterbrush sites | | Sagebrush sites | | Sagebrush sites | |
|---|---|---|---|---|---|---|
| | INRA NE | Grandview | INRA | Round Butte | INRA | Haystack |
| Juniper | 8.7[a] | 16.9[b] | 10.5[a] | 12.4[a] | 10.5[a] | 19.0[b] |
| Sagebrush | 2.1[a] | 0.0[a] | 15.4[a] | 15.5[a] | 15.4[a] | 16.5[a] |
| Bitterbrush | 9.8[a] | 11.8[a] | | | | |
| Thurbers needlegrass | 4.6[a] | 6.4[a] | 2.9[a] | 2.8[a] | 2.9[a] | 0.0[b] |
| Bluebunch wheatgrass | 2.5[a] | 3.1[a] | 3.4[a] | 4.6[a] | 3.4[a] | 0.9[b] |
| Idaho fescue | 4.8[a] | 0.0[b] | 2.6[a] | 0.4[b] | 2.6[a] | 5.5[b] |
| Sandberg's bluegrass | 3.9[a] | 2.3[a] | 2.8[a] | 4.3[a] | 2.8[a] | 5.5[a] |
| Cheatgrass | 2.6[a] | 2.1[a] | 0.1[a] | 0.3[a] | 0.1[a] | 0.0[a] |
| Slender fescue | 0.6[a] | 0.8[a] | 0.4[a] | 0.5[a] | 0.4[a] | 0.1[a] |
| Total Grass | 19.3[a] | 14.7[a] | 12.2[a] | 12.9[a] | 12.2[a] | 12.0[a] |
| Bareground/rock | 22.2[a] | 28.0[b] | 35.2[a] | 26.3[a] | 35.2[a] | 37.7[a] |
| Litter/moss/lichen | 57.5[a] | 53.3[a] | 55.9[a] | 58.7[a] | 55.9[a] | 49.5[a] |

than IRNA, and there were no significant differences in litter cover (Table 4).

## Discussion

Our study was first undertaken to determine vegetation change over a 30 yr period on a semi-relic site. The major differences noted include greater tree and shrub cover, and a more even mix of grass species rather than the dominance of bluebunch wheatgrass and cheatgrass noted by Driscoll (1964a). We also found sagebrush present in the juniper/bitterbrush/wheatgrass whereas Driscoll (1964a) reported none. Driscoll (1964a) described two plant associations on IRNA, whereas we identified the possibility of three. The juniper/bitterbrush/wheatgrass South and West plots (Tables 1, 2) are more closely aligned with the juniper/sagebrush/wheatgrass association described by Driscoll (1964b). Possible descriptions for this third association are juniper/sagebrush/wheatgrass - bitterbrush phase, or a transition of the juniper/bitterbrush/wheatgrass association to a juniper/sagebrush-bitterbrush/wheatgrass codominant association. The separation of big sagebrush and bitterbrush is partially attributed to different soil structure, texture, and rooting depth (Driscoll 1964a). Big sagebrush adapts to a variety of soil profiles, including those found on the juniper/bitterbrush/wheatgrass sites (Frischknecht 1963). In any case, big sagebrush is becoming a more prominent member of both associations.

Driscoll (1964a) noted substantial differences in bare ground and litter cover between the two associations, with more bare ground in the juniper/sagebrush/wheatgrass plots and more litter in the juniper/bitterbrush/wheatgrass plots (Tables 1, 2). We found a less dramatic variation between the two associations than was recorded in the 1960s.

Our results for tree, shrub and general grass cover for the juniper/sagebrush/wheatgrass association are similar to Knapp and Soulé (1996). An important benefit when comparing the results of the two recent studies is that the effectiveness of the two plot location methods can be evaluated. Using newly established plots within a defined area rather than re-measuring plots from an earlier study will provide the opportunity for more areas to be studied.

The major difference between our results and Knapp & Soulé (1996) was in specific grass species found. They reported substantially more bluebunch wheatgrass and somewhat less Idaho fescue than we found on the same association. Our plots supported a fairly even mix of bluebunch wheatgrass, Thurber's needlegrass, Idaho fescue, and Sandberg's bluegrass (Table 1). This difference could be due to differences in macroplot location, but we did find a similarly even mix of grasses in the juniper/bitterbrush/wheatgrass association and on our comparison sites.

Juniper cover increased slowly, a reminder of the slowness of change in this ecosystem (Table

3). Our 1995 measurements of 10.5% cover in the juniper/sagebrush/wheatgrass association agreed closely with those reported by Knapp and Soulé (1996) of 9.8% cover. Driscoll (1964a) reported a greater difference in juniper cover between the two associations than we found, but measuring exact tree cover is problematic due to the unevenness of distribution, site selection bias, inability to identify small trees in aerial photographs, and the lack of precision in the method of measurement used. We observed young juniper trees rising above the shrub layer throughout IRNA, and Soulé and Knapp (2000) reported that juvenile juniper populations on IRNA represented as much as 81% of the total population.

Our study of the more accessible, less pristine comparison sites showed slightly higher tree and shrub cover and lower grass cover than found on IRNA (Table 4), which may be due to more livestock grazing and human impact on the comparison sites (Madany and West 1983). Notable differences in grass cover included an absence of Idaho fescue on the Grandview site, low cover of this grass on the Round Butte Dam Overlook site, but greater cover on Haystack Butte site.

The general lack of fire is a probable influence on the trend toward a greater presence of woody species on IRNA and on the comparison sites. Aerial photographs from 1944 to 1995 show no major fire disturbance during this 51 yr period. Driscoll (1964a) reported that charred stumps and other signs of fire were common on IRNA. We observed evidence of small spot fires, however, they appeared to have minimal influence on the overall vegetation pattern being few in number and widely scattered. Our findings agree with West et al. (1979) and Eddleman and Miller (1992) that woody vegetation may out-compete perennial grasses unless periodic fires are present in the system.

In general our data agreed with the theory that without disturbance, especially without fire, woody vegetation will increase in cover (West et al. 1984, Barbour et al. 1999). In analyzing the vegetation by canopy layer, our study found more tree and shrub cover and less grass and forb cover in both plant associations than reported by Driscoll (1964a).

The building of Round Butte Dam in 1964 to create Lake Billy Chinook might be considered a disturbance, but the effect of the lake on IRNA vegetation is unknown and probably subtle. Climatic data from Metolius Station show no trend toward more moderate temperatures or higher humidity, but the station, located ~10 km east of IRNA may be outside the lake influence zone. Weather data, analyzed from decade to decade between the 1950s and the 1990s showed no measurable trends. Annual temperature was stable and precipitation, while varying widely from year to year, showed no significant pattern of change.

Although access to IRNA is limited, other major threats to its native vegetation may likely be increased human use and exotic weed invasions. Driscoll (1964a) expressed concern about the presence of the alien cheatgrass, but our study and Knapp and Soulé (1996) found less cheatgrass cover than in the 1960s. Medusahead, while not found in the microplots, is also present on IRNA as is another alien annual grass, red brome.

Previously recognized plant associations on IRNA are in the process of change. Without a major disturbance we expect the directional change toward more woody vegetation to continue. If fires were reintroduced into the ecosystem this would likely set back woody plants to give grasses and forbs greater presence. The present fire policy on IRNA recently agreed upon by the joint managers, the USDA Forest Service, Bureau of Land Management, and Oregon State Parks, is one of non-intervention (Ron Halvorson, BLM, Prineville, Oregon, personal communication). This policy may serve to reintroduce fire to IRNA and provide interesting new vegetation dynamics to study.

An important aspect of this study was to provide documentation with which to compare future studies on IRNA and in the nearby grasslands. Ongoing examination of vegetation cover, land use histories, climatic data, and fire events in this area will continue to broaden our understanding of vegetation dynamics and the complex process of plant succession over time.

## Literature Cited


Anderson, J. E., and R. E. Holte. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. Journal of Range Management 34:25-29.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1999. Terrestrial Plant Ecology. 3rd Edition. Benjamin/Cummings, Santa Barbara, California.

Doescher, P. S., R. F. Miller, and A. H. Winward. 1984. Soil chemical patterns under eastern Oregon plant communities dominated by big sagebrush. Soil Science Society of America Journal 48:659-663.

Driscoll, R. S. 1962. Characteristics of some vegetation-soil units in the juniper zone in central Oregon. Ph.D. Dissertation, Oregon State University, Corvallis, Oregon.

Driscoll, R. S. 1964a. A relict area on the central Oregon juniper zone. Ecology 45:345-353.

Driscoll, R. S. 1964b. Vegetation-soil units in the central Oregon juniper zone. USDA Forest Service Research Paper PNW-19. Pacific Northwest Research Station, Portland, Oregon.

Eddleman, L. E., and P. M. Miller. 1992. Potential impacts of western juniper on the hydrologic cycle. Pages 176-180 *In* W. P. Clary (compiler), Proceedings-symposiom on ecology and management of riparian shrub communities. USDA Forest Service General Technical Report INT-289. Intermountain Research Station, Ogden, Utah.

Fox, M. A. 1995. The Island Research Natural Area: a vegetation study with time and location comparisons. M. S. Thesis, Oregon State University, Corvallis, Oregon.

Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Frischknecht, N. C. 1963. Contrasting effects of big sagebrush and rubber rabbitbrush on production of crested wheatgrass. Journal of Range Management 16:70-74.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington.

Hobbs R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324-337.

Hyder, D. N., and F. A. Sneva. 1956. Herbage response to sagebrush spraying. Journal of Range Management 9:34-38.

Knapp, P., and P. T. Soulé. 1996. Vegetation change and the role of atmospheric $CO_2$ enrichment on a relict site in central Oregon: 1960-1994. Annals of the Association of American Geographers 86:387-411.

Knapp, P., and P. T. Soulé. 1998. Recent *Juniperus occidentalis* (western juniper) expansion on a protected site in central Oregon. Global Change Biology 4:347-357.

Madany, M. H. and N. E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64:661-667.

Miller, R. F., J. M. Seufert, and M. R. Haferkamp. 1986. The ecology and management of bluebunch wheatgrass (*Agropyron spicatum*): a review. Station Bulletin 669. Agricultural Experiment Station., Oregon State University, Corvallis, Oregon.

Moessner, K. E. 1960. Training handbook: basic techniques in forest photo interpretation. USDA Forest Service Intermountain Research Station, Ogden, Utah.

Oregon Climate Service. 2002. Oregon State University. Corvallis, Oregon. Available online at http://www.ocs.orst.edu.

Orr, E. L., and W. N. Orr. 1999. Geology of Oregon, 5th Edition. Kendall/Hunt, Dubuque, Iowa.

Poulton, C. E., and E. W. Tisdale. 1961. A quantitative method for the description and classification of range vegetation. Journal of Range Management 14:13-21.

Sneva, F. A., L. R. Rittenhouse, P. T.Tueller, and P. Reece. 1984. Changes in protected and grazed sagebrush-grass in eastern Oregon, 1937 to 1974. Station Bulletin 663, Agricultural Experiment Station, Oregon State University, Corvallis, Oregon.

Soulé, P. T., and P. Knapp. 2000. *Juniperis occidentalis* (western juniper) establishment history on two minimally disturbed research natural areas in central Oregon. Western North American Naturalist 60:26-33.

USDA Natural Resources Conservation Service. 2002. Soil survey of upper Deschutes River area, Oregon, including parts of Deschutes, Jefferson, and Klamath Counties. Available online at http://ice.or.nrcs.usda.gov/website/soils/reports_htm/oregon/UpperDeschutes.htm.

West, N. E., F. D. Provenza, P. S. Johnson, and M. K. Owens. 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. Journal of Range Management 37:262-264.

West, N. E., K. H. Rea, and R. O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. Ecology 60:376-388.

Whitson, T. D. 1991. Weeds of the West. Western Society of Weed Science, Laramie, Wyoming.



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# Carbon Storage in Subalpine Tree Islands, North Cascade Range, Washington

## Abstract

Quantifying carbon (C) pools in subalpine systems is an important first step to understanding the effects of climatic variability on terrestrial C dynamics in temperate mountainous regions. We quantified C and other soil characteristics for tree islands and the vegetatively distinct meadows surrounding the tree islands at three subalpine sites (Thornton Lakes, Heather Pass, and Harts Pass) in the North Cascade Range. O-horizon C storage ranged from 0.6 to 2.6 kg $m^{-2}$ in meadows and from 3.1 to 5.8 kg $m^{-2}$ in tree islands. Gradual vegetative transitions and similar soil depths result in similar quantities of mineral soil C in meadows and tree islands at Thornton Lakes (8.1 vs. 8.3 kg $m^{-2}$) and Heather Pass (7.9 vs. 10.3 kg $m^{-2}$). Abrupt vegetative transitions and deeper soils may allow more mineral-soil C to be stored in meadows than tree islands at Harts Pass (14.1 vs. 7.2 kg $m^{-2}$), although these mean values are not significantly different due to high variability in soil profile properties. Mean C concentrations in mineral soil horizons have no consistent relationship with vegetation type (tree island vs. meadow). Total ecosystem C storage is higher in tree islands (range, 35.1 to 98.5 kg $m^{-2}$) than meadows (range, 7.4 to 18.0 kg $m^{-2}$), primarily due to large amounts of C in the aboveground biomass of trees. Consequently, the effects of future climatic variability on C storage in subalpine ecosystems will largely depend on the degree to which conditions that limit tree island expansion (winter snowpack, summer drought) are affected.

## Introduction

Spatial patterns of carbon (C) storage are highly variable in the forest-meadow mosaic of subalpine parklands (Bockheim 1972, Holtmeier and Broll 1992, Prichard et al. 2000, Van Miegroet et al. 2000). Tree regeneration and growth in this zone are limited by high summer temperatures at dry locations and a deep and long-lasting snowpack at wet locations (Agee and Smith 1984, Graumlich 1991, Vogt et al. 1989, Powers and Edmonds 1992, Rochefort et al. 1994, Woodward et al. 1995, Ettl and Peterson 1995, Rochefort and Peterson 1996). Consequently, abrupt vegetation differences occur as trees establish in islands on ridges and topographical convexities, landforms that have a lengthened growing season because they are either windswept of snow or experience early snowmelt (Fonda and Bliss 1969, Woodward et al. 1995, Rochefort and Peterson 1996, Peterson 1998). Along with variation in vegetation distribution and microtopography, associated differences exist in the quantity and quality of stored C (Prichard et al. 2000).

Large and small scale variability in C storage has been analyzed as a function of climatic influences on biotic and pedological conditions (Bockheim 1972, Sims and Nielsen 1986, Vogt et al. 1989, Christ and David 1996, Prichard et al. 2000). Western slopes of the North Cascade Range in Washington have a maritime climate characterized by low temperatures and a long period of rain, snow, and extensive cloud cover in winter. Summer temperatures are mild and precipitation is low. Eastern Cascade slopes also receive substantial winter precipitation, but temperatures are higher, snowmelt is earlier, and the period of low soil moisture in summer is more prolonged than on the western slopes. Consequently, the resulting variation in factors such as length of growing season, species distribution, and quantity and distribution of soil water may result in varied patterns of C storage at large spatial scales.

At local scales, C storage is influenced by microclimatic differences due to landform (concavity vs. convexity) (Bockheim et al. 2000) and vegetation physiognomy (forest vs. meadow) (Belsky and del Moral 1982, Van Miegroet et al. 2000). In the North Cascades, it appears that once trees establish on topographical convexities they ameliorate local environmental conditions and change successional pathways through several

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feedback mechanisms. Trees augment early snowmelt on convexities by acting as black bodies. In these high-snowpack environments, the presence of trees alters snowdrift (Lowery 1972, Holtmeier and Broll 1992, Pauker and Seastedt 1996) and snowmelt (Van Miegroet et al. 2000) patterns sufficiently to facilitate tree regeneration. Snowpack and relatively decay-resistant coniferous litter also modify extreme changes in soil temperature year round (Edmonds 1980, Powers and Edmonds 1992). Consequently, the tree island understory is dominated by species different from those in the adjacent meadow. Litter from the understory vegetation then provides additional organic matter and nutrients to the soil as seedlings establish or existing trees propagate vegetatively in this more suitable substrate (Holtmeier and Broll 1992). These biotic and microclimatic differences probably are responsible for documented changes in pedological features and the distribution of C as tree islands expand, shrink, or migrate within subalpine parklands (Bockheim 1972, Douglas 1972, Holtmeier and Broll 1992, Pauker and Seastedt 1996, Van Miegroet et al. 2000).

Under the current climatic regime, subalpine ecosystems may represent a considerable long-term C sink. Residence time of soil C is higher under low-temperature conditions due to low microbial activity, slow decomposition (Edmonds 1980, Kirschbaum 1995) and higher C allocation to belowground components. A consistent supply of soil water, from rainfall and snowmelt, may leach C into deeper horizons where it exists in more stable forms and is less subject to mineralization (Kuramoto and Bliss 1970, Vogt et al. 1989, Stone et al. 1993, Richter et al. 1995, Christensen et al. 1999). Reduced soil moisture may retard this process for a short time during the summer months, but it can also reduce decomposition in the upper soil profile. Changes in the current climatic regime likely will alter the quality and quantity of C stored in subalpine systems.

Soils in subalpine ecosystems are poorly studied despite their widespread distribution in western North America and their potential importance to long-term C storage. Quantifying C distribution in these ecosystems will help refine current estimates of C in forest ecosystems and improve our understanding of climatic, vegetative and pedological influences on soil C storage. We hypothesized that soil C storage in subalpine parklands in northern Washington would differ between tree islands and the surrounding meadow in response to vegetation and microtopographical variation. The objective of this study was to compare soil C storage, soil chemical properties, and C storage in biomass between tree islands and the adjacent meadows at three sites in the subalpine parkland zone of the North Cascade Range in Washington.

## Methods

### Study Area

The study was conducted in subalpine parklands at Thornton Lakes, Heather Pass, and Harts Pass in the North Cascade Range (Figure 1, Table 1). For the purposes of this study, subalpine parkland is defined as the zone between closed canopy forests and alpine meadows, characterized by tree islands surrounded by subalpine meadow (Figure 2). Three tree islands were selected for study at each site. Tree islands were representative of each site in terms of vegetation (species composition, size, and structure), slope (gradient and topography), aspect, and elevation.

The general area was last glaciated in the late Pleistocene and is characterized by broad, steep-sided, U-shaped valleys, smaller hanging valleys, and glacial cirques. The elaborate amalgam of igneous, metamorphic, and sedimentary rocks underlying this glacially carved landscape is visible in the many rock outcrops that dot the study sites. Bedrock materials at Thornton Lakes and Heather Pass are granitic. Interbedded layers of sandstone, shale, and conglomerate underlie Harts Pass.

Approximately 8.6% of the North Cascade Range is in the subalpine parkland zone (Gaines et al. 1994), a 300 to 500 m elevational band about 1,400 to 2,200 m above sea level. The majority of annual precipitation falls in the winter as snow. Mild summer temperatures generally ensure that winter snowpacks persist until July. The short summer growing season is typically a relatively dry period. The North Cascades are an orographic barrier to marine influences from the west resulting in less precipitation and slightly higher temperatures on the eastern slopes. As a result, subalpine parklands are at higher elevations on the east side than on the west.

Soils generally are shallow Spodosols and Inceptisols. Soils at Thornton Lakes and Heather Park are loamy to sandy (sometimes skeletal),

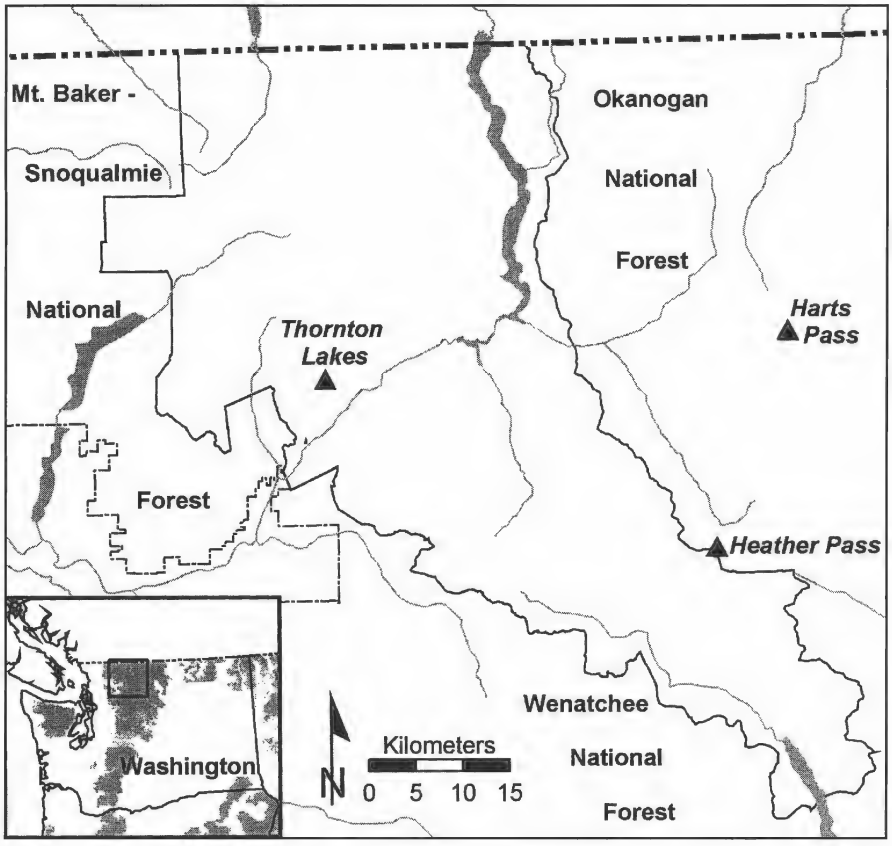


Figure 1. Locations of the three study sites in the North Cascade Range.

TABLE 1. Summary of site characteristics and mean annual climatic data. Climatic data are from the closest representative sites for 1995-97; Stevens Pass (elev. 1240 m) represents Thornton Lakes, Rainy Pass (elev. 1457 m) represents Heather Pass. Source: Natural Resources Conservation Service SNOTEL network.

| | Thornton Lakes | Heather Pass | Harts Pass |
|---|---|---|---|
| Elevation (m) | 1593 | 1847 | 1971 |
| Landform | Ridge above valley wall | Ridge above valley wall | Valley sideslope |
| Slope (%) | 18 – 25 | 13 – 30 | 13 - 22 |
| Mean tree island size (m) | 9 x 13 | 6 x 13 | 7 x 12 |
| Basal area ($m^2$ $ha^{-1}$) | 74.3 – 100.2 | 40.2 – 224.0 | 118.0 – 225.0 |
| Age of oldest tree (yr) | 105 – 140 | 212 – 245 | 98 - 117 |
| Climate | | | |
| Temperature (°C) | | | |
| January | -4.4 | -6.7 | -7.8 |
| July | 12.4 | 11.2 | 8.3 |
| Precipitation (cm) | | | |
| Total | 304.3 | 189.0 | 149.1 |
| Max. snow depth | 240.5 | 281.0 | 320.5 |

Figure 2. The tree island-meadow mosaic at Harts Pass.

mixed, frigid Lithic Haplocryods, Typic Humicryods and Lithic Humicryods. Soils at Harts Pass are loamy to sandy (sometimes skeletal), mixed, frigid Typic Haplocryods, Typic Humicryods, Lithic Humicryods, Typic Dystrocryepts, and Lithic Dystrocryepts (Soil Survey Staff 1999).

The most abundant tree island species at the study sites are mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*), and Pacific silver fir (*Abies amabilis*) to the west of the Cascade crest, with big huckleberry (*Vaccinium membranaceum*) and alpine blueberry (*Vaccinium deliciosum*) most abundant in tree-island understories. To the east of the Cascade crest, subalpine fir, Engelmann spruce (*Picea engelmannii*) and subalpine larch (*Larix lyallii*) comprise tree island overstories, and understories are increasingly dominated by subalpine fir. Meadow species surrounding tree islands are primarily big huckleberry on the western slopes, alpine blueberry, and red heather (*Phyllodoce empetriformis*) near the crest and a mixture of herbaceous species dominated by timber danthonia (*Danthonia intermedia*), sedges (*Carex* spp.), and alpine bluegrass (*Poa alpina*) on the eastern slopes.

## Sampling Design

Three tree island/meadow pairs were sampled at each site. Soil pits were excavated to bedrock or to depths where stone fragments prohibited further digging, and the soil profiles were sampled and described (Tables 2-4). Mineral and organic

TABLE 2. Representative descriptions of tree island and meadow soil profiles at Thornton Lakes.

| Horizon | Depth (cm) | Color (moist) | Texture/structure | Rock volume (%) | Roots |
|---|---|---|---|---|---|
| **Thornton Lakes tree island interior #2A—Lithic Humicryod** | | | | | |
| O | 9-0 | | | | |
| E | 0-5 | 7.5YR 5/2 | Loamy sand<br>Subangular blocky | 10 | Many very fine and fine; common medium |
| Bs1 | 5-20 | 7.5YR 3/4 | Sandy loam<br>Subangular blocky | 10 | Few very fine and fine; common medium |
| Bs2 | 20-31 | 7.5YR 3/4 | Gravelly sandy loam<br>Subangular blocky | 30 | Few very fine and fine; common medium |
| R | 31+ | | | | |
| **Thornton Lakes tree island/meadow #2D—Lithic Dystrocryept** | | | | | |
| O | 9-0 | | | | |
| E | 0-8 | 5YR 3/1 | Loamy sand<br>Subangular blocky | 0 | Common very fine, fine and medium; few coarse |
| Bhs1 | 8-13 | 7.5YR 3/4 | Gravelly sandy loam<br>Subangular blocky | 20 | Many very fine; common fine |
| Bs2 | 13-20 | 7.5YR 4/4 | Gravelly sandy loam<br>Subangular blocky | 40 | Few very fine and fine |
| R | 20+ | | | | |

TABLE 3. Representative descriptions of tree island and meadow soil profiles at Heather Pass.

| Horizon | Depth (cm) | Color (moist) | Texture/structure | Rock volume (%) | Roots |
|---|---|---|---|---|---|
| **Heather Pass tree island interior #1A—Typic Humicryod** | | | | | |
| O | 10-0 | | | | |
| E | 0-11 | 10YR 6/1 | Loamy sand<br>Subangular blocky | 0 | Common fine and medium; few coarse |
| Bhs1 | 11-18 | 7.5YR 2/2 | Sandy loam<br>Subangular blocky | 5 | Common fine; few medium |
| Bs2 | 18-35 | 7.5YR 3/4 | Sandy loam<br>Subangular blocky | 5 | Common fine and medium; few coarse |
| Bs3 | 35-55 | 7.5YR 3/4 | Sandy loam<br>Subangular blocky | 0 | Common fine; few medium and coarse |
| R | 55+ | | | | |
| **Heather Pass tree island/meadow #1D—Lithic Humicryod** | | | | | |
| O | 7-0 | | | | |
| E | 0-5 | 5YR 6.5/1 | Loamy sand<br>Subangular blocky | 0 | Many very fine; few fine and medium |
| Bhs1 | 5-7 | 7.5YR 3/4 | Loamy sand<br>Crumb | 10 | Common fine and medium |
| Bs2 | 7-17 | 7.5YR 4/6 | Sandy loam | 10 | Few very fine and medium |
| R | 17+ | | | | |

TABLE 4. Representative descriptions of tree island and meadow soil profiles at Harts Pass.

| Horizon | Depth (cm) | Color (moist) | Texture/structure | Rock volume (%) | Roots |
|---|---|---|---|---|---|
| **Harts Pass tree island interior #2A—Lithic Humicryod** | | | | | |
| O | 4-0 | | | | |
| E/Bh | 0-7 | 10YR 4/2.5 | Sandy loam<br>Crumb | 10 | Many very fine and fine; few medium and coarse |
| Bs1 | 7-15 | 7.5YR 2.5/2 | Gravelly sandy loam<br>Subangular blocky | 30 | Many very fine and fine; few medium |
| Bs2 | 15-27 | 10YR 2/2 | Very gravelly sandy loam<br>Crumb | 70 | Many very fine and fine; few medium |
| CB | 27-37 | 2.5YR 5/2.5 | Very gravelly sandy loam<br>Crumb | 90 | Few very fine and fine |
| R | 37+ | | | | |
| **Harts Pass tree island/meadow #2D—Typic Dystrocryept** | | | | | |
| O | 0.5-0 | | | | |
| B1 | 0-30 | 10YR 3/2.5 | Gravelly sandy loam<br>Subangular blocky | 30 | Many very fine and fine; common medium |
| B2 | 30-53 | 10YR 3/3 | Gravelly sandy loam<br>Subangular blocky | 40 | Many very fine and fine; common medium |
| BC | 53-74 | 2.5YR 5/4 | Very gravelly sandy loam<br>Subangular blocky | 70 | Common very fine; few fine and medium |

soils were sampled along transects that originated at what was estimated to be the portion of the island with the oldest trees, determined either by the presence of large living trees or standing dead trees, and terminated in the meadow. Three soil pits were excavated within each tree island; at the transect origin, midway between the origin and the tree island edge, and at the tree island edge. Meadow samples were excavated where vegetation most represented the entire meadow,

beyond the drip line of the tree islands, and where no wood or tree roots occurred. Within each soil profile, one sample was taken from each mineral horizon, and the organic sub-horizons were composited as one sample, although depth was measured for each sub-horizon. Eight additional samples of the composited organic (O) horizon were extracted along the sampling transect to obtain a finer spatial resolution than the soil pits allowed. A 20-cm diameter cylinder was used to extract each O-horizon sample.

Each tree island was mapped and the vegetation measured. Within the tree island each tree taller than 1.37 m (diameter at breast height [dbh]) was mapped and species, height, and dbh recorded. Trees <1.37 m were counted and their species noted. Heights and diameters of standing dead trees, and the length, end and midpoint diameters of woody debris >7.5 cm diameter were recorded. Shrubs and herbaceous vegetation were quantified by estimating percent cover within each 3x3-m grid cell. Finally, three randomly located vegetation samples were extracted from a 9-$m^2$ quadrat in the meadow so that comparisons could be made between tree island and meadow. For each of these samples, all aboveground and belowground biomass within a 20-cm diameter circular frame was collected. Belowground samples were collected to the depth where stone fragments prohibited further extraction and included both live and dead roots. Aboveground samples included all live and dead vegetation.

## Soil Analysis

Composited O-horizon samples were air dried, ground in a Wiley mill with a 20-mesh screen, then were more finely ground with a mortar and pestle to ensure homogenization for C and N analysis. Subsamples were analyzed for C and nitrogen (N) (g $kg^{-1}$) with a CHN analyzer at the Forest Soils Laboratory, University of Washington.

Prior to analysis, all mineral soil samples were air dried, and sieved through a 2-mm screen to remove rocks and roots. Soluble extractions from the soil subsamples were required for the determination of both exchangeable cations and cation exchange capacity (CEC). Extractions were prepared by saturating 2.5 g of air-dried, < 2-mm mineral soil subsamples with 60 ml of 1.0 M $NH_4OAc$. Samples were then placed in a mechanical extractor overnight to remove $NH_4OAc$ from saturated exchange sites. The resulting solutions were collected and analyzed for exchangeable cation concentration by atomic absorption ($Ca^{2+}$ and $Mg^{2+}$) or atomic emission ($Na^+$ and $K^+$) flame spectrophotometry at the Soil Characterization Laboratory, University of Missouri. Steam distillation and titration were then used to measure the adsorbed $NH_4^+$ and determine CEC (Soil Survey Staff 1992). Base saturation (BS) was calculated as the percent of CEC occupied by exchangeable cations.

Available phosphorus (P) was extracted using the Bray 1 absorbed P method (Olsen and Sommers 1982, Soil Survey Staff 1992).

Samples from prospective Bs and Bhs horizons were analyzed for percent iron (Fe) and percent aluminum (Al) to verify spodic criteria (Soil Survey Staff 1992). Two grams of air-dried, < 2-mm soil were saturated with 200 ml of 0.2 M ammonium oxalate. These suspensions were mixed on a mechanical shaker for 4 hr in the dark and then filtered through a Whatman #42 filter. The resulting filtrates were analyzed for Fe and Al concentrations using inductively coupled argon plasma emission spectroscopy.

Soil acidity for each horizon was determined with a pH meter. Deionized water was mixed with <2-mm mineral soil samples (2:1) prior to determination of acidity.

Bulk density (g $cm^{-2}$) was determined by extracting an intact soil aggregate from each mineral horizon and measuring its volume displacement in water. Oven-dry mass of each sample soil aggregate was later measured in the lab. Bulk density of each horizon was calculated after accounting for the mass and volume of the >2-mm fraction.

Soil C mass (g $kg^{-1}$) for organic horizons was calculated by multiplying C concentration (g $kg^{-1}$) by organic layer mass (kg $m^{-2}$). Soil C mass for mineral soil was calculated as:

$$C\ (kg\ m^{-2}) = \Sigma\ [\text{organic C concentrations of } <2\text{-mm material } (g\ kg^{-1}) \times \text{bulk density of } <2\text{-mm material} \times \text{horizon depth (m)} \times (1 - \text{rock volume [\%]}/100\%) \times 10^4\ cm^2 m^{-2} \times 10^{-6} kg^2 g^{-2}]$$

where the summation is across the horizons within the soil profile (Homann et al. 1995). Soil C is understood to be of organic nature because carbonates (source of inorganic C) are not found in

the parent materials of the study region, and soils are strongly acidic.

### Biomass Sampling and C Calculations

Aboveground and belowground tree biomass was estimated using field measurements and BIOPAK (Means et al. 1994), which calculates biomass based on relationships from empirical data (height and dbh) for tree species in the Cascade Range. Large woody debris biomass was calculated using equations based on Harmon and Sexton (1996). Carbon content was assumed to be 50% of biomass values.

Aboveground and belowground meadow biomass was quantified by calculating mass of C per unit area (kg $m^{-2}$) at each site by using a mean biomass value from the three meadow samples. Belowground root samples were prepared by washing samples over a 1-mm screen to remove residual soil. Aboveground and belowground samples were air-dried, weighed, ground in a Wiley mill with a 20-mesh screen, then finely ground with a mortar and pestle to ensure homogenization. Samples were then analyzed in a CHN analyzer for percent C.

### Statistical Analysis

Data were analyzed using a balanced, cross-nested three-factor mixed-effects ANOVA model without replication. Treatment (each sampling location along the transect) is a random effect. Site (Thornton Lakes, Heather Pass and Harts Pass) is a random effect, and Island (TH1, TH2 . . . HA3) is a random effect nested within site. The following variables were thus analyzed: C storage (mineral soil, belowground biomass, aboveground biomass, and large woody debris), soil chemical properties (pH, CEC, %BS, C, N, available P, Ca, Na, Mg, K and C:N) and soil depth. Mean soil chemical property values for each soil pit were weighted by thickness and rock content of individual horizons. Organic soil C was similarly analyzed, except total number of treatment classes is 11. Treatment effect differences were considered significant at $P < 0.05$.

## Results

### Soil Profile Characteristics

Soil profile characteristics varied considerably between sites and vegetation types (i.e., tree island vs. ecotone) (Tables 2-4). Differences in O-horizon depth were not significant between sampling locations, although O horizons in Harts Pass meadows appeared considerably thinner than in the tree islands. No consistent patterns of horizonization, either within sites or vegetation types were observed, but some similarities were found.

Thornton Lakes and Heather Pass soils typically contained strongly expressed E horizons over one or more spodic horizons (Tables 2, 3). E horizons were determined by color, and Bs horizons were determined by color and Fe and Al content (Soil Survey Staff 1999). Upper mineral soil horizons at Harts Pass (typically Bh/E) were not strongly expressed and frequently have high organic matter content. Additionally, horizonization was less distinct and podzolization was less strongly expressed at Harts Pass. At Thornton Lakes and Heather Pass, Bs horizons were directly over bedrock, stones or boulders, while skeletal BC and CB horizons comprised the lower profile at Harts Pass.

Soil texture was consistent (loamy sands and sandy loams) across the study sites, however, mineral soil depth and rock content varied considerably (Table 5). Soil profiles were relatively shallow, ranging from 17 to 74 cm, with large differences in soil depth often present within each site and vegetation type. Although differences in soil depth between tree islands and meadows were not significant at all sites, meadow soils were visually deeper than tree island soils at Harts Pass. Rock content increased with depth at all sites in 33 of the 36 examined profiles. Upper horizons at Thornton Lakes and Heather Pass typically contained 0-10% rock fragments and increased to more than 30% in the lowest horizons. Harts

TABLE 5. Soil profile depth (± one standard error) by vegetation type.

| Site | Vegetation type | |
|---|---|---|
| | Tree island | Meadow |
| | Organic horizons (cm) | |
| Thornton Lakes | 9.0 ± 5.7 | 5.0 ± 4.0 |
| Heather Pass | 9.7 ± 6.2 | 5.8 ± 3.9 |
| Harts Pass | 6.4 ± 4.6 | 1.0 ± 0.5 |
| | Mineral soil (cm) | |
| Thornton Lakes | 35.3 ± 2.0 | 31.3 ± 11.0 |
| Heather Pass | 37.1 ± 3.4 | 36.3 ± 16.9 |
| Harts Pass | 42.6 ± 8.4 | 63.3 ± 10.5 |

Pass soils had a higher rock content, with 10-20% in both the E and upper B horizons and 90% in the lower B and C horizons.

## Soil Carbon

There was no indication that mineral soil C storage or concentration (Tables 6, 7) differed significantly along the sampling transect at any site. Mineral soil C storage in Harts Pass meadows may be greater than within tree islands, although a larger sample size is needed to detect such differences.

Carbon storage in O horizons ranged from 0.6 to 2.6 kg $m^{-2}$ in meadows and from 3.1 to 5.8 kg $m^{-2}$ in tree islands (Table 4). Gradual vegetative transitions and similar soil depths resulted in similar quantities of mineral soil C in meadows and tree islands at Thornton Lakes (8.1 vs. 8.3 kg $m^{-2}$) and Heather Pass (7.9 vs. 10.3 kg $m^{-2}$). Abrupt vegetative transitions and deeper soils may have affected C storage in mineral soils in meadows and tree islands at Harts Pass (14.1 vs. 7.2 kg $m^{-2}$), although these mean values were not significantly different due to high variance in soil profile properties. Mean C concentrations in mineral soil horizons had no consistent relationship with vegetation type (tree island vs. meadow).

Total ecosystem C storage was higher in tree islands (range, 35.1 to 98.5 kg $m^{-2}$) than meadows

TABLE 6. Ecosystem C pools (kg $m^{-2}$) (± one standard error) by vegetation type.

| Ecosystem C pool | Vegetation type: Tree island | Meadow |
|---|---|---|
| | Organic horizons (kg $m^{-2}$) | |
| Thornton Lakes | 5.8 ± 3.6 | 2.6 ± 1.6 |
| Heather Pass | 3.1 ± 2.7 | 2.0 ± 1.6 |
| Harts Pass | 3.9 ± 3.2 | 0.6 ± 0.9 |
| | Mineral soil (kg $m^{-2}$) | |
| Thornton Lakes | 8.3 ± 4.8 | 8.1 ± 4.8 |
| Heather Pass | 10.3 ± 6.4 | 7.9 ± 3.4 |
| Harts Pass | 7.2 ± 2.8 | 14.1 ± 3.0 |
| | Belowground biomass (kg $m^{-2}$) | |
| Thornton Lakes | 4.3 ± 1.7 | 3.7 ± 1.2 |
| Heather Pass | 6.8 ± 6.3 | 1.3 ± 0.4 |
| Harts Pass | 10.3 ± 6.7 | 1.4 ± 0.4 |
| | Large woody debris (kg $m^{-2}$) | |
| Thornton Lakes | 6.6 ± <0.1 | na |
| Heather Pass | 25.7 ± 8.3 | na |
| Harts Pass | 7.4 ± 18.6 | na |
| | Aboveground biomass (kg $m^{-2}$) | |
| Thornton Lakes | 19.7 ± 1.9 | 0.7 ± 0.2 |
| Heather Pass | 21.6 ± 10.6 | 0.6 ± 0.2 |
| Harts Pass | 28.9 ± 12.8 | 0.2 ± 0.1 |
| | Total (kg $m^{-2}$) | |
| Thornton Lakes | 43.3 ± 5.8 | 15.4 ± 3.2 |
| Heather Pass | 70.7 ± 34.1 | 10.9 ± 3.4 |
| Harts Pass | 61.5 ± 22.8 | 16.0 ± 2.2 |

TABLE 7. Chemical properties of mineral soil by (± one standard error) vegetation type.

| Ecosystem C pool | Vegetation type: Tree island | Meadow |
|---|---|---|
| | pH ($H_2O$) | |
| Thornton Lakes | 4.46 ± 0.16 | 4.33 ± 0.08 |
| Heather Pass | 4.37 ± 0.26 | 4.82 ± 0.21 |
| Harts Pass | 5.05 ± 0.61 | 5.43 ± 0.27 |
| | Cation exchange capacity (cmol $kg^{-1}$) | |
| Thornton Lakes | 28.1 ± 9.2 | 34.8 ± 29.1 |
| Heather Pass | 33.5 ± 13.3 | 25.7 ± 9.2 |
| Harts Pass | 31.7 ± 9.4 | 30.2 ± 12.4 |
| | Base saturation (%) | |
| Thornton Lakes | 1.7 ± 1.3 | 1.0 ± 0.6 |
| Heather Pass | 3.8 ± 2.7 | 1.3 ± 1.1 |
| Harts Pass | 19.7 ± 19.1 | 17.2 ± 22.6 |
| | Carbon (g $kg^{-1}$) | |
| Thornton Lakes | 44.8 ± 20.0 | 69.3 ± 54.0 |
| Heather Pass | 77.4 ± 35.2 | 57.9 ± 25.9 |
| Harts Pass | 72.6 ± 13.4 | 70.2 ± 28.3 |
| | Nitrogen (kg $m^{-2}$) | |
| Thornton Lakes | 1.2 ± 0.5 | 1.8 ± 1.3 |
| Heather Pass | 1.8 ± 0.7 | 1.4 ± 0.3 |
| Harts Pass | 4.4 ± 1.4 | 4.8 ± 2.4 |
| | Available phosphorus (mg $kg^{-1}$) | |
| Thornton Lakes | 9.6 ± 5.1 | 11.4 ± 2.2 |
| Heather Pass | 4.6 ± 1.8 | 4.9 ± 4.8 |
| Harts Pass | 12.7 ± 10.3 | 3.7 ± 2.2 |
| | Calcium (mg $kg^{-1}$) | |
| Thornton Lakes | 21.8 ± 29.5 | 5.1 ± 8.7 |
| Heather Pass | 76.6 ± 64.0 | 21.9 ± 27.0 |
| Harts Pass | 1290 ± 1560 | 1200 ± 1890 |
| | Magnesium (mg $kg^{-1}$) | |
| Thornton Lakes | 0.4 ± 0.7 | 0.6 ± 0.5 |
| Heather Pass | 1.5 ± 1.0 | 0.3 ± 0.5 |
| Harts Pass | 3.4 ± 2.9 | 3.1 ± 3.8 |
| | Sodium (mg $kg^{-1}$) | |
| Thornton Lakes | 4.3 ± 7.5 | 6.3 ± 5.5 |
| Heather Pass | 1.8 ± 5.4 | 4.4 ± 4.0 |
| Harts Pass | 6.5 ± 9.8 | 7.7 ± 13.3 |
| | Potassium (mg $kg^{-1}$) | |
| Thornton Lakes | 41.7 ± 14.6 | 29.7 ± 6.0 |
| Heather Pass | 41.0 ± 19.1 | 10.6 ± 6.8 |
| Harts Pass | 63.0 ± 21.8 | 48.9 ± 17.6 |
| | Carbon:nitrogen | |
| Thornton Lakes | 37.3 ± 4.8 | 38.5 ± 8.1 |
| Heather Pass | 43.0 ± 5.9 | 41.4 ± 9.1 |
| Harts Pass | 16.5 ± 2.5 | 14.6 ± 1.4 |

(range, 7.4 to 18.0 kg $m^{-2}$), primarily due to large amounts of C in the aboveground biomass of trees. These values are based on a combination of empirical data on soil C and biomass C calculated from allometric relationships.

## Discussion

### Soil Carbon

We expected that greater aboveground litter production combined with the recalcitrant nature of coniferous organic matter would lead to more C storage in the tree island mineral soils. However, within-site variability in total mineral soil C appears to be most strongly related to vegetative characteristics and soil depth and is probably related to microsite differences in parent materials, rock content, decomposition rates, and aboveground and belowground productivity. Other studies have found deeper O horizons that store more C within tree islands in studies that compare soils between subalpine tree islands and meadows (Bockheim 1972, Holtmeier and Broll 1992, Prichard et al. 2000, Van Miegroet et al. 2000). Tree islands modify microclimate and moisture conditions (Holtmeier and Broll 1992) in their interiors, possibly slowing the rate of decomposition and encouraging greater organic matter accumulations.

At Thornton Lakes and Heather Pass, saplings and huckleberry and heather species at the edges of the tree islands are widely dispersed such that the islands merge gradually into meadow. Consequently, factors that influence C storage, such as microclimate, decomposition rate and aboveground and belowground litter production (Stevenson 1986, Prescott et al. 1989), are probably relatively uniform between the tree island and meadow. Conversely, differences in these factors between Harts Pass tree islands and meadows are likely greater because the vegetative transitions are abrupt. Additionally, Harts Pass meadows are dominated by productive graminoid and other deep-rooted herbaceous species (Figure 3) that cycle large amounts of belowground C to soils (Kuramato and Bliss 1970, Anderson and Coleman 1985, Prichard et al. 2000).

Glaciation, high precipitation, low temperatures, and colluvial activity on steep slopes have influenced pedogenesis in the study area resulting in shallow soils across all sites. Mineral soils are deeper in meadows than tree islands at Harts Pass and consequently store more C by area, unlike Thornton Lakes and Heather Pass where soil depth is similar among vegetation types (Table 3). Additionally, our profile descriptions indicate that soils surrounding Harts Pass tree islands contain more fine roots in deeper horizons, which

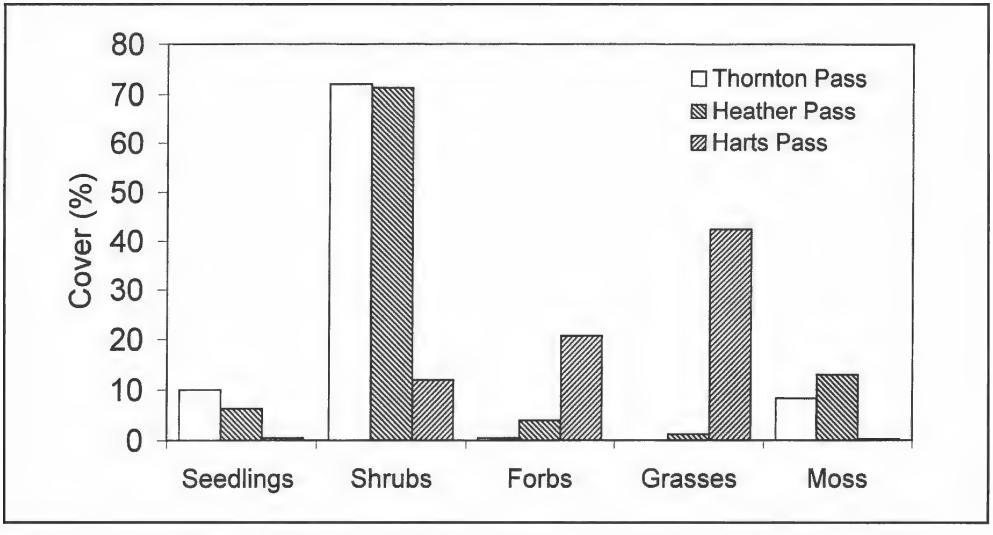


Figure 3. Meadow vegetation at each site characterized by percent cover of vegetation type.

probably contribute to the larger quantities of mineral soil C in Harts Pass meadows.

Podzolization, driven by high soil moisture, low temperatures, and acidic coniferous and ericaceous litter (Ugolini et al. 1988, Holtmeier and Broll 1992, David et al. 1995, Li et al. 1998), occurs at all sites and is most prevalent at Thornton Lakes and Heather Pass. At Thornton Lakes and Heather Pass, where the Bs is typically the deepest horizon, there are no consistent patterns of decreasing C concentration with depth (Figure 4). BC and CB horizons at Harts Pass contain less C than the overlying B horizon. Because C often exists in more stable forms deeper in the soil, high C concentrations in Bhs and Bs horizons found in this study may result in large quantities of long-term C storage (Oades 1988, Stone et al. 1993, Hammer et al. 1995, Richter et al. 1995, Christensen et al. 1999).

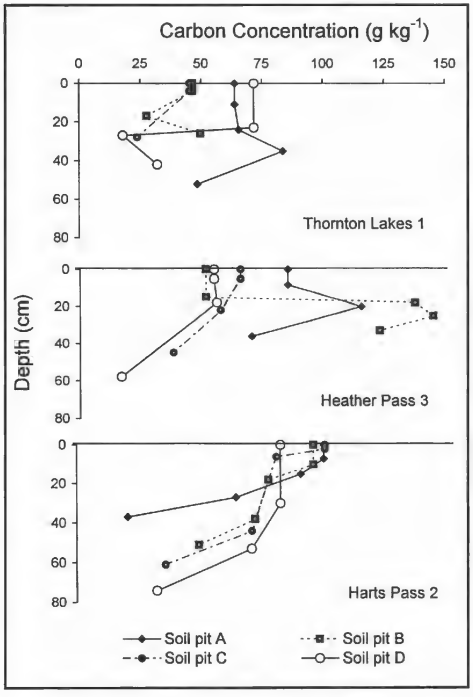


Figure 4. Mineral soil C concentration (g $kg^{-1}$) in each of the four soil profiles sampled in and around selected tree islands. Each curve represents a different soil profile along the sampling transect; A, B and C are from tree islands; D is from tree island/meadow.

Similar to other studies of montane and subalpine soils (Grier 1973, McNabb et al. 1986, Sims and Nielson 1986, Homann et al. 1995), mean mineral soil C concentrations are high at all sites, ranging from 44.8 to 77.4 g $kg^{-1}$ (Table 5). However, total soil C quantities are lower than in other Pacific Northwest forest ecosystems (Table 6). Fewer rock fragments (Grier et al. 1981, Homann et al. 1995), deeper profiles (Edmonds and Chappell 1994, Homann et al 1995), and more stable landforms (Grier et al. 1981) may have contributed to higher quantities of C storage in the mineral soil in these studies compared to our observations in the North Cascade Range. Reduced aboveground biomass production combined with colluvial activity on steep slopes may also reduce long-term surficial storage of C in subalpine ecosystems of the North Cascades. However, common subalpine geomorphological features, such as cirque basins, toe slopes and local concavities, can accumulate sediments rich in C (Richter et al. 1995, Christensen et al. 1999).

Prichard et al. (2000) compared dry (continental climate) vs. wet (maritime climate) subalpine systems in the Olympic Mountains, Washington. Higher mineral soil C in meadows than forests in the dry system was attributed to the dominance of graminoid species in the meadows. Conversely, forests stored more mineral soil C in the wet system, probably a result of differences in overall productivity, organic matter accumulation and a deep, long-lasting snowpack that hinders decomposition. In the Colorado Front Range (continental climate) (Holtmeier and Broll 1992), C concentrations in the A horizon were higher in meadows than tree islands, but only on the leeward side of the islands. This pattern presumably reflects the influence of wind on the distribution of organic material in that system. In the Wasatch Mountains of northern Utah, C concentrations were higher under tree island canopies than in meadows, but only in the upper 5 cm of mineral soil Van Miegroet et al. 2000). They cite the importance of aboveground litter production in determining relative C concentrations.

## Soil Chemical Properties

Coniferous vegetation and thick organic horizon accumulations, as are found in tree islands, enhance nutrient release through mineralization (Weaver and Forcella 1979, Edmonds 1980,

Sommerfield et al. 1993). There are tendencies in the data that support the notion that cation concentrations are slightly higher in tree islands than meadows (Table 7), although there are no significant differences. For example, mean Ca concentration is higher in tree islands than meadows at all sites, and base saturation, Mg, and K are higher in Heather Pass tree islands. Aside from these trends, the soil chemistry of tree islands and meadows is similar. Due to vegetation continuity, some of the factors that control mineralization of soil nutrients (litter quality, soil temperature and soil moisture) are probably fairly uniform between tree islands and meadows at Thornton Lakes and Heather Pass, resulting in some similar soil chemistry characteristics.

At Harts Pass, higher temperatures may lead to earlier snowmelt and higher productivity of graminoid meadow vegetation that has been associated with higher nutrient status (Edmonds 1980, Anderson and Coleman 1985). Additionally, Harts Pass soils generally have higher nutrient content than at Thornton Lakes and Heather Pass, as well as low C:N ratios that may favor microbial activity and nutrient availability (Van Cleve and Moore 1978, McGill and Cole 1981, Tate and Salcedo 1988, David et al. 1995). Weathering of sedimentary parent material (interbedded sandstones and shales) at Harts Pass, in contrast to granitic bedrock at the other sites, likely contributes significant quantities of cations. Soil C retention at Harts Pass may be facilitated by these higher nutrient concentrations, because base cations, particularly Ca, enhance organo-metallic and clay complexes that bind C (Anderson et al. 1975, Protz 1983).

Concentrations of most soil nutrients are relatively low, particularly at Thornton Lakes and Heather Pass, compared to soils in other subalpine ecosystems (Weaver and Forcella 1979, Holtmeier and Broll 1992, Prichard et al. 2000). Low base saturation and low soil nutrient concentrations are caused by leaching by soil water derived from high precipitation, including deep and persistent snowpacks. Cation concentrations tend to decrease with soil depth at all sites, which suggests that organic matter in upper horizons is an important source of soil nutrients (Schoenau and Bettany 1987, Vogt et al. 1989, Doskey and Bertsch 1997, Prichard et al. 2000). Soils at all sites are extremely to moderately acidic (pH 3.65 to 6.11), and acidity generally decreases with depth at all sites.

### Ecosystem Carbon

Tree islands store more ecosystem C than meadows, however C distribution within ecosystem components varies between tree islands and meadows (Table 4). In tree islands, aboveground biomass (especially tree stems), large woody debris, and organic horizons store more C than in meadows. Length of growing season, snowpack duration and soil nutrient content affect aboveground productivity and thereby influence the amount of C stored in aboveground biomass, as well as litter production and retention (Grier et al. 1981, Boone et al. 1988, Powers and Edmonds 1992). Earlier snowmelt and a higher soil nutrient content that supports vegetative productivity probably contribute to the relatively large amounts of total C found in aboveground biomass at Harts Pass tree islands. Because of the east-side location of Harts Pass, soil moisture in the meadows is lower for longer periods than at the other two sites, likely resulting in the dominance of deep-rooting forbs and grasses that grow deeper into the soil profile. Although no evidence of recent fire or heavy grazing by large herbivores was found at any of the sites, these and other variables may also affect long-term C storage and distribution in subalpine systems.

Ecosystem C storage and distribution in this study are similar to a study in the Olympic Mountains (Prichard et al. 2000) (Table 8). Carbon storage in tree islands in this study is also similar to other studies of mature, closed-canopy, upper-slope forests in the Pacific Northwest (Grier et al. 1981, Boone et al. 1988). However, the discontinuous nature of forest cover in subalpine parklands results in lower total ecosystem C than in closed canopy forests.

Variability in ecosystem C storage in subalpine parklands in the North Cascade Range is linked to the distribution of tree-island and meadow vegetation and pedologic features such as soil depth. The presence of trees results in higher C storage in aboveground biomass, woody debris and organic soil (O horizons) in tree islands than in meadows. Mineral soil C storage, however, is similar in tree islands and meadows where there is a gradual vegetation transition between trees and dominant meadow species. Differences between mineral soil C in tree islands and mead-

TABLE 8. Comparison of mineral soil C in Pacific Northwest studies.

| Ecosystem | Vegetation type | Mineral soil C ($kg\ m^{-2}$) | Sampling depth | Reference |
|---|---|---|---|---|
| **Subalpine parkland** | | | | |
| North Cascade Range, Washington | Tree island | 8.6[1] | Rock/bedrock | This study |
| | Tree island/meadow | 10.0[1] | | |
| Olympic Mountains, Washington | Forest | 8.5 | Rock/bedrock | Prichard et al. (2000) |
| | Meadow | 8.7 | | |
| **High-elevation montane forest** | | | | |
| Cascade Range, Washington | Forest | 13.7 | 70 cm | Grier et al. (1981) |
| Montane forest, Western Oregon | Forest | 15.0 | 50 cm–rock | Homann et al. (1995) |
| **Low elevation montane forest** | | | | |
| Cascade Range, Oregon, Washington | Forest | 10.2–30.9 | C horizon | Edmonds and Chappell (1994) |
| Cascade Range, Oregon | Forest | 4.5–6.5 | 100 cm | Grier and Logan (1977) |

[1]Based on the mineral soil mean value for tree islands and meadows in Table 7.

ows are more likely to be detected where vegetation transitions are abrupt. Because tree islands often establish on topographical convexities underlain by rock, tree island soils may be relatively shallower than meadow soils. Consequently meadow C storage is enhanced simply by greater soil volume. Additionally, meadows dominated by deep-rooting graminoid vegetation whose rate of C turnover exceeds aboveground inputs to the soil store more mineral soil C than tree islands.

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## Literature Cited

Agee, J. K., and L. Smith. 1984. Subalpine tree establishment after fire in the Olympic Mountains, Washington. Ecology 65:810-819.

Anderson, D. W., and D. C. Coleman. 1985. The dynamics of organic matter in grassland soils. Journal of Soil and Water Conservation 40:211-216.

Anderson, J. U., O. F. Bailey, and D. Rai. 1975. Effects of parent material on genesis of borolls and boralfs in south-central New Mexico Mountains. Soil Science Society of America Proceedings 39:901-904.

Belsky, J., and R. del Moral. 1982. Ecology of an alpine-subalpine meadow complex in the Olympic Mountains, Washington. Canadian Journal of Botany 60:779-788.

Bockheim, J. G. 1972. Effects of alpine and subalpine vegetation on soil development, Mt. Baker, Washington. Ph.D. Dissertation, University of Washington, Seattle, Washington.

Bockheim, J. G., P. W. Birkeland, and W. L. Bland. 2000. Carbon storage and accumulation rates in alpine soils: evidence from Holocene chronosequences. Pages 185-196 *In* R. Lal, J. M. Kimble and B. A. Stewart (editors), Global Climate Change and Cold Region Ecosystems. Lewis Publishers, Boca Raton, Forida.

Boone, R. D., P. Sollins, and K. Cromack Jr. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. Ecology 69:714-722.

Christ, M. J., and M. B. David. 1996. Temperature and moisture effects on the production of dissolved organic carbon in a spodosol. Soil Biology and Biochemistry 28:1191-1199.

Christensen, T. R., S. Johnson, T. V. Callaghan, and M. Havstrom. 1999. On the potential $CO_2$ released from tundra soils in a changing climate. Applied Soil Ecology 11:127-134.

David, M. B., G. F. Vance, and A. J. Krzyszowska. 1995. Carbon controls on spodosol nitrogen, sulfur, and phosphorus cycling. Pages 329-353 *In* W. W. McFee

and J. M. Kelly (editors), Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Madison, Wisconsin.

Doskey, M. G., and P. M. Bertsch. 1997. Transport of dissolved organic matter through a sandy forest soil. Soil Science Society of America Journal 61:920-927.

Douglas, G. W. 1972. Subalpine plant communities of the western North Cascades, Washington. Arctic and Alpine Research 4:147-166.

Edmonds, R. L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. Canadian Journal of Forest Research 10:327-337.

Edmonds, R. L., and H. N. Chappell. 1994. Relationships between soil organic matter and forest productivity in western Washington and Oregon. Canadian Journal of Forest Research 24:1101-1106.

Ettl, G. J., and D. L. Peterson. 1995. Extreme climate and variation in tree growth: individualistic response in subalpine fir (*Abies lasiocarpa*). Global Change Biology 1:231-241.

Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the subalpine and montane zones, Olympic Mountains, Washington. Ecological Monographs 39:271-301.

Gaines, W. L., R. H. Naney, P. H. Morrison, J. R. Eby, G. F. Wooten, and J. A. Almack. 1994. Use of Landsat multispectral scanner imagery and geographic information systems to map vegetation in the North Cascades Grizzly Bear Ecosystem. International Conference on Bear Research and Management 9:533-547.

Graumlich, L. 1991. Subalpine tree growth, climate and increasing $CO_2$: an assessment of recent growth trends. Ecology 72:1-11.

Grier, C. C. 1973. Organic matter and nitrogen distribution in some mountain heath communities of the Source Lake Basin, Washington. Arctic and Alpine Research 3:26-267.

Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs 47:373-400.

Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Canadian Journal of Forest Research 11:155-167.

Hammer, R. D., G. S. Henderson, R. Udawatta, and D. K. Brandt. 1995. Soil organic carbon in the Missouri forest-prairie ecotone. Pages 201-232 *In* W. W. McFee, and J. M. Kelly (editors), Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Madison, Wisconsin.

Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication no. 20. Long-Term Ecological Research Network Office. Seattle, Washington.

Holtmeier, F. K., and G. Broll. 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, U.S.A. Arctic and Alpine Research 24:216-228.

Homann, P. S., P. Sollins, H. N. Chappell, and A. G. Stangenberger. 1995. Soil organic carbon in a mountainous, forested region: relation to site characteristics. Soil Science Society of America Journal 59:1468-1475.

Kirschbaum, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic storage. Soil Biology and Biochemistry 27:753-760.

Kuramoto, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs 40:317-345.

Li, S.-Y., Z.-S. Chen, and J.-C. Liu. 1998. Subalpine loamy spodosols in Taiwan: characteristics, micromorphology, and genesis. Soil Science Society of America Journal 62:710-716.

Lowery, R. F., 1972. Ecology of subalpine zone tree clumps in the North Cascade Mountains of Washington. M.S. Thesis, University of Washington, Seattle, Washington.

McGill W. B., and C. V. Cole. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26:267-286.

McNabb, D. H., K. Cromak Jr., and R. L. Fredriksen. 1986. Variability of nitrogen and carbon in surface soils of six forest types in the Oregon Cascades. Soil Science Society of America Journal 50:1037-1041.

Means, J. E., H. A. Hansen, G. J. Koerper, P. B. Alaback, and M. W. Klopsch. 1994. Software for computing plant biomass – BIOPAK users guide. USDA Forest Service General Technical Report PNW-GTR-340. Pacific Northwest Research Station, Portland, Oregon.

Oades, J. M. 1988. The retention of organic matter in soils. Biogeochemistry 5:35-70.

Olsen, S. R., and L. E. Sommers. 1982. Phosphorus. Pages 403-430 *In* A. L. Page, R. H. Miller, and D. R, Keeney (editors), Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. American Society of Agronomy, Madison, Wisconsin.

Pauker, S. J., and T. R. Seastedt. 1996. Effects of tree islands on soil carbon storage in tundra ecosystems. Ecology 77:2563-2567.

Peterson, D. L. 1998. Climate, limiting factors and environmental change in high-altitude forests of Western North America. Pages 191-208 *In* M. Beniston, and J. L. Innes (editors), The Impacts of Climate Variability on Forests. Springer, Berlin, Germany.

Powers, R. F., and R. L. Edmonds. 1992. Nutrient management of subalpine *Abies* forests. Pages 28-42 *In* H. N. Chappell, R. E. Weetman, and R. E. Miller (editors), Forest fertilization: Sustaining and improving nutrition and growth of western forests. Institute of Forest Resources, University of Washington, Seattle, Washington.

Prescott, C. E., J. P. Corbin, and D. Parkinson. 1989. Input, accumulation and residence times of carbon, nitrogen and phosphorus in four Rocky Mountain coniferous forests. Canadian Journal of Forest Research 19:489-498.

Prichard, S. J., D. L. Peterson, and R. D. Hammer. 2000. Carbon distribution in subalpine forests and meadows of

the Olympic Mountains, Washington. Soil Science Society of America Journal 64:1834-1845

Protz, R. 1983. Calcium-dominated organans in humic podzols from the Hudson and James Bay lowlands of Ontario (Canada). Canadian Journal of Forest Research 30:171-177.

Richter, D. D., D. Markewitz, C. G. Wells, H. L. Allen, J. K. Dunscombe, K. Harrison, P. R. Heine, A. Stuanes, B. Urrego, and G. Bonani. 1995. Carbon cycling in a loblolly pine forest: implications for the missing carbon sink and for the concept of soil. Pages 233-252 *In* W. W. McFee and J. M. Kelly (editors), Carbon Forms and Functions in Forest Soils, Soil Science Society of America, Madison, Wisconsin.

Rochefort, R. M., R. L. Little, A. Woodward, and D. L. Peterson. 1994. Changes in subalpine tree distribution in western North America: a review of climatic and other causal factors. The Holocene 4:89-100.

Rochefort, R. M., and D. L. Peterson 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, U.S.A. Arctic and Alpine Research 28:52-59.

Schoenau, J. J., and J. R. Bettany. 1987. Organic matter leaching as a component of carbon, nitrogen, phosphorus and sulfur cycles in a forest, grassland, and gleyed soil. Soil Science Society of America Journal 51:646-651.

Sims, Z. R., and G. A. Nielsen. 1986. Organic carbon in Montana soils as related to clay content and climate. Soil Science Society of America Journal 50:1269-1271.

Soil Survey Staff. 1992. Soil survey lab methods manual. Soil survey investigations report 42. USDA Soil Conservation Service, Lincoln, Nebraska.

Soil Survey Staff. 1999. Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys. USDA Handbook. 436. 2nd edition. U.S. Government Printing Office, Washington, D.C.

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Sommerfield, R.A., A.R. Mosier, and R.C. Musselman. 1993. $CO_2$, $CH_4$ and $N_2O$ flux through a Wyoming snowpack and implications for global budgets. Nature 361:140-142.

Stone, E.L., W.G. Harris, R.B. Brown, and R.J. Kuehl. 1993. Carbon storage in Florida spodosols. Soil Science Society of America Journal 57:179-182.

Stevenson, F.J. 1986. Cycles of Soil: Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients. Wiley, New York.

Tate, K. R., and I. Salcedo. 1988. Phosphorus control of soil organic matter accumulation and cycling. Biogeochemistry 5:99-107.

Ugolini, F. C., R. Dahlgren, S. Shoji, and T. Ito. 1988. An example of andosolization and podzolization as revealed by soil solution studies, southern Hakkoda, northeastern Japan. Soil Science 145:111-125.

Van Cleve, K., and T. A. Moore. 1978. Cumulative effects of nitrogen, phosphorus, and potassium fertilizer additions on soil respiration, pH, and organic matter content. Soil Science Society of America Journal 42:121-124.

Van Miegroet, H., M. T. Hysell, and A. D. Johnson. 2000. Soil microclimate and chemistry of spruce-fir tree islands in northern Utah. Soil Science Society of America Journal 64:1515-1525.

Vogt, K. A., E, Moore, S. Gower, D. Vogt, D. Sprugel, and C. Grier. 1989. Productivity of upper slope forests in the Pacific Northwest. Pages 137-163 *In* D. Perry (editor), Maintaining the Long-term Productivity of Pacific Northwest Ecosystems. Timber Press, Portland, Oregon.

Weaver, T., and F. Forcella. 1979. Seasonal variation in soil nutrients under six Rocky Mountain vegetation types. Soil Science Society of America Journal 43:589-593.

Woodward, A., E. G. Schreiner, and D. G. Silsbee. 1995. Climate, geography, and tree establishment in subalpine meadows of the Olympic Mountains, Washington, U.S.A. Arctic and Alpine Research 27:217-225.

## Book Review

### Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore

Kenneth Logan and Linda Sweanor, 2001, Island Press, Washington, D.C., 463 pages. ISBN 1-55963-867-2. Hardcover $70, Paperback $45

This book reports results of a 10 year study of pumas (*Puma concolor*) in the San Andres Mountains of southcentral New Mexico. The goal of this study was to provide "basic biological and ecological information...for pumas and their prey." The work was "mission-oriented" and "describes in detail the natural history of pumas in that (desert) environment." Logan and Sweanor used three research objectives to guide their work: 1) describe and quantify puma population dynamic, 2) describe and quantify puma social organization, and 3) describe and quantify relationships between puma and mule deer (*Odocoileus hermionus crooki*). The purpose of this book is to present the findings of their research and then to "explain" the evolutionary ecology of pumas. The book consists of 21 chapters organized into five parts: "Setting the Stage"; "Puma Life History Strategies and Population Dynamics"; "Puma Behavior and Social Organization"; "Puma-prey Relationships"; and "Pumas and People."

Concerning the goal of the original research, the authors gathered an impressive data base on the basic natural history of pumas living in a desert environment. This was done with the help of a large number of others, from state and federal personnel to students and volunteers. I applaud all involved for this tremendous field effort. As emphasized, this was the first of such work in this environment and does fill an obvious gap in our knowledge of puma biology.

Relative to the findings of their study, the most impressive to me was the lack of difference they found with results of other studies. In almost all cases, the means of their observations fell within the range reported by others, from Wyoming to Canada to Nevada. This conformity is significant because it indicates the uniformity in the ecology and behavior of pumas across a wide variety of habitats, which now including the desert, and geographic regions, which now reach to the Mexican border! Like its genetics, the puma is emerging as a rather behaviorally and ecologically uniform species and that findings from diverse habitats and regions can likely be more amply applied to management strategies in different areas.

Apart from the value of this book containing the vast amount of information from their study, I did find the presentation of these data to be somewhat distracting. It was never clear for which audience they were writing: the popular press or the scientific community. At times the authors seem to be playing toward the general lay audience, especially with the section on "Life Afield." Their detailed description of their field camps and operations is aimed at the nonscientist—e.g., they had to truck in all their supplies. For field scientists, this is regular stuff and of little interest. They also frequently used vernacular terms or slang, e.g., "The...tail is cranked ...prey, hustling..." (page 19) or "...females monopolizing the sexual favors... (page 92)—all definitely aimed at a lay audience. Also, many of their descriptions of methods and explanations of ideas were put in extremely simplistic terms, again, I assume for the lay audience. Their presentation of the data, i.e., tables and figures, on the other hand, was quite formal, as would be expected in a scientific work. Often, however, the microanalysis of their data, such as long complicated discussions of individual pumas, would be difficult to follow by any reader.

Apart from the presentation of their impressive data set, a large portion of the book is devoted to the evolutionary ecology of pumas. Much of this incorporates their findings in a review and reevaluation of the extensive data from many excellent past studies. In doing so, as admitted, the authors engaged in a lot of speculation on their part. A little speculation in science is a good thing but these authors seemed to delve into it quite extensively and freely, often with little support from their own data. For example, much of what they speculate in many chapters is based on the idea that young males disperse to avoid inbreeding. However, they give good evidence that young males disperse because they cannot compete with



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their fathers nor new incoming males; they get killed (pages 122-123), supporting the competition hypotheses (page 240). Also they provide evidence that resident males will mate with their daughters (page 102), which is no different genetically from a son mating with his mother, thereby refuting the inbreeding hypothesis. Nonetheless, they still conclude that young males disperse to avoid inbreeding and then proceed to speculate on the consequences of this.

Sometimes, too, Logan and Sweanor seemingly draw conclusions directly opposite of their data. A case in point is whether pumas were controlling bighorn sheep in their study. They present data that puma predation on collared bighorn sheep was low (10 animals in 10 years, page 347), with 7 (70%) of these sheep being infected with scabies or in poor health, i.e., possible compensatory mortality. Additionally, the authors report that "...puma predation by itself apparently did not stop the sheep population from growing during our research tenure" (page 354). In light of all that, they still conclude that "...puma predation was a strong limiting factor..." (page 354). It is too easy and common to blame the puma for declining sheep populations and the authors seemed to have fallen into this trap. This is unfortunate because it can mask the real reasons for sheep declines.

The last part, "Pumas and People," attempts to put all the information together in some form of conservation management of pumas in the West. I found their idea of zone management interesting. They do point out several problems that would still exist with this method. One, for example, is that zone management would require detailed monitoring of puma numbers, which still is not possible. However, it is a good starting point and hopefully will lead to meaningful discussions on the sound management of pumas.

In summary, this book provides an exhaustive analysis of data from an impressive field study of pumas in the desert environment. It indeed does fill a gap in our information base on pumas. The data presented in this book will be of interest to puma biologists in all regions. Regarding the evolutionary ecology and conservation of pumas, the ideas presented by the authors are often highly speculative but that should provide good fuel for future discussions and research.

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# NORTHWEST SCIENCE

*Information for Authors*

## Purpose and Scope

The Northwest Scientific Association represents the natural and social sciences in the Pacific Northwest. The pages of *Northwest Science* are open to original and fundamental research in the basic and applied natural and social sciences. All submissions are refereed, usually by two reviewers and an Associate Editor. Papers are welcome from authors outside of the Pacific Northwest.

## Web Site Information

Authors should visit the Northwest Scientific Association web site to obtain the most recent version of Information for Authors. The web site address is: www.vetmed.wsu.edu/org_NWS/NWSci_Home.htm

## Articles

Articles present the results of new and original research, and generally are 6–20 journal pages long. Authors must contact the Editor in advance before submitting longer papers. Authors are encouraged to use line numbering for the original submission, which will help speed up the review process.

## Notes

The purpose of Notes is to publish papers typically less than five journal pages long. Suggested topics include preliminary results, new methods, significant range extensions, and perhaps taxonomic observations. There is no specific format or content required for Notes, but all will be peer-reviewed and must be scientifically creditable. Authors may contact the Editor about the suitability of manuscripts to be published as Notes.

## Northwest Science Forum

This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum may not be peer-reviewed so that publication is expedited. The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

## Manuscripts

### General Instructions

Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten in 12 point Times New Roman font, on 8.5" x 11" paper, double-spaced throughout (including Abstract, Acknowledgements, Literature Cited, Tables, and Figure captions). Allow one-inch margins around the page. The format and style of manuscripts should conform to general usage in recent issues, and should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgements)
- Literature Cited
- Footnotes
- Tables
- Figure Captions
- Figures

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In that situation, lowercase letters will be used. Do not hyphenate words at the ends of lines. Words to be italicized will be typed in italic rather than underlined.

## Title Page

The first page of the manuscript should contain:

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- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running footer (for right-hand pages)
- Total number of tables and figures
- List the name, full address, telephone number, fax number, and e-mail address of the author to whom correspondence should be sent. Use a footnote to indicate a corresponding author other than the senior author. For example: "[1]Author to whom correspondence should be addressed."

## Abstract

The second page of the manuscript contains the Abstract. Authors are strongly encouraged to give the abstract proper attention. The abstract briefly summarizes the study, so that it is quickly accessible to the general readership of the journal. The abstract must be written in complete sentences and may not exceed 250 words. Because of the diverse disciplines and readership served by the journal, the abstract should include the following three parts: 1) a statement of the purpose of the study, indicating the reasons behind its undertaking; 2) a statement describing the experimental design or approach and a summary of the results; 3) a summarizing sentence or two regarding the larger significance of the research.

## Text

Start the text on the third page, and use continuous pagination. Do not start new sections on new pages.

Literature citations within the text should contain the author's name and year of publication, using formats A and B. Multiple citations of authors within the same parentheses will be listed in chronological order.

- Format A:

...studied by Jones (1998)...

...studied by Smith and Brown (1999)...

...studied by Smith et al. (2000)...(if more than two authors in a citation)

- Format B:

...was previously investigated (Smith 1991, Jones 1995, Harris 2000)

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Numbers from one to nine will be spelled out, while Arabic numerals will be used for numbers 10 and larger. Exceptions to this convention are: 1) a series of mixed numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 5 g, 0.7 mm, 3 $m^2$). Arabic numerals will also be used for dates, times, page numbers, and percentages.

Authors are requested to use the International System of Units (SI). Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1998). Use leading zeroes with all numbers <1 (e.g., 0.12), including probability values with "*P*" capitalized and italicized (e.g., $P \leq 0.05$). Please note these examples of other conventions followed by *Northwest Science*: 20th Century, 3rd Edition, Douglas-fir, dbh, sec, min, hr, day (or d), wk, mo, yr. Please do not use the construction "and/or" because "or" invariably will suffice.

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These should be kept to an absolute minimum, because they do not meet the requirements for first disclosure as defined by the Council of Biology Editors. If used, the full name and affiliation of the person being quoted is required. *Personal communications are cited in the text,* not in Literature Cited. For example:

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Only the *first letter* of the *first word* of journal articles, technical reports, theses, symposia papers, and technical bulletins are capitalized. First letters of *major words* in book titles are capitalized. All authors and editors of a title will be listed in the bibliographic citation. Use "et al." only in the body of the text, never in the Literature Cited section.

Citations should be double-spaced and listed in alphabetical order at the end of the article. *Note that the names of all sources are spelled out.* The only exceptions are the commonly used abbreviations USDA, USDI, EPA, and USA. The abbreviations USDA and USDI must be followed by the name of the agency (e.g., USDA Forest Service; USDI Bureau of Land Management).

Double-check literature to ensure that citations in the text and in Literature Cited agree. On one submitted copy, indicate by green check marks on each citation in the text and each citation in Literature Cited that the references have been double-checked.

The general format for citations is:

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- Use a space between initials and names.
- Short bar. Beginning with the Fall 2001 issue, *Northwest Science* will no longer use a short bar for repeated entries by the same author.
- Issue numbers are unnecessary.
- Double-check each citation to ensure that it conforms to the *Northwest Science* format.

Typical examples of *Northwest Science* format conventions for Literature Cited are as follows:

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Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus*. Journal of Mammalogy 51:310-326.

Broadbooks, H. E. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus*. American Midland Naturalist 83:472-488.

Cêska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

### *Monographs or books*

Edmunds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, New York. *(number of pages unnecessary)*

Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.

### *Papers in proceedings or symposia*

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pages 363-393 *In* H. Barnes (editor), Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, UK.

Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

### *Theses, dissertations, and articles in press*

Donald, D. B. 1971. The limnology of the plankton of three temporary ponds in Alberta. M.S. Thesis, University of Calgary, Calgary, Alberta.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. Ph.D. Dissertation, University of Utah, Salt Lake City, Utah.

Dunwiddie, P. W. *In Press*. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science. *(if the publication date is unknown or uncertain)*

Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecological Applications 10: (*in press*). *(if the publication date is known and certain).*

### *Technical bulletins*

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin Number 60. Washington State University.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

### *Online (web) references*

USDA Forest Service. 1998. Fire effects information system. Prescribed Fire and Fire Effects Research Work Unit, Rocky Mountain Research Station, Missoula, Montana. Available online at www.fs.fed.us/database/feis/

### *Unpublished Reports*

Unpublished reports often contain useful data that contribute to the development of the study being

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Kraft, G. F. 1967. Annual report on the status of Lake Whatcom. Unpublished report on file at Western Washington University, Bellingham, Washington.

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Footnotes to the text are discouraged. In most cases, the potential footnote information can easily be incorporated in the text. If footnotes are unavoidable, they must be numbered consecutively and clearly indicated in the text.

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### Figures

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- ...experimental sites as indicated in Figure 2...
- ...correlation between temperature and biomass (Table 3)...

Artwork, photos, and other illustrative material cannot be returned to the author.

## Experimental Design and Statistical Analyses

In the Methods section, clearly describe the experimental design and identify all components (e.g., treatments, blocks, independent and dependent variables, subsamples) so that reviewers and readers understand all procedures. At the end of this section in the Methods state that the level of significance was set at $P = 0.05$ before the research began, so that readers know decisions about significance were based on that value. Do not set significance levels >0.05 for the research. Authors may show other probabilities (e.g., $P < 0.01$, $P < 0.001$) when results are reported for further information, but the decisions must be made on $P = 0.05$. Do not report $P$ values smaller than $P < 0.001$). Do not report $P$ values for differences that were not significant.

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Each author or group of authors must sign a Publication Agreement provided by the Editor before their submission will be published in the journal.

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Page charges are currently $65 per printed page for members of the Northwest Scientific Association, and $80 for non-members. Authors wishing to become members may contact the Treasurer.

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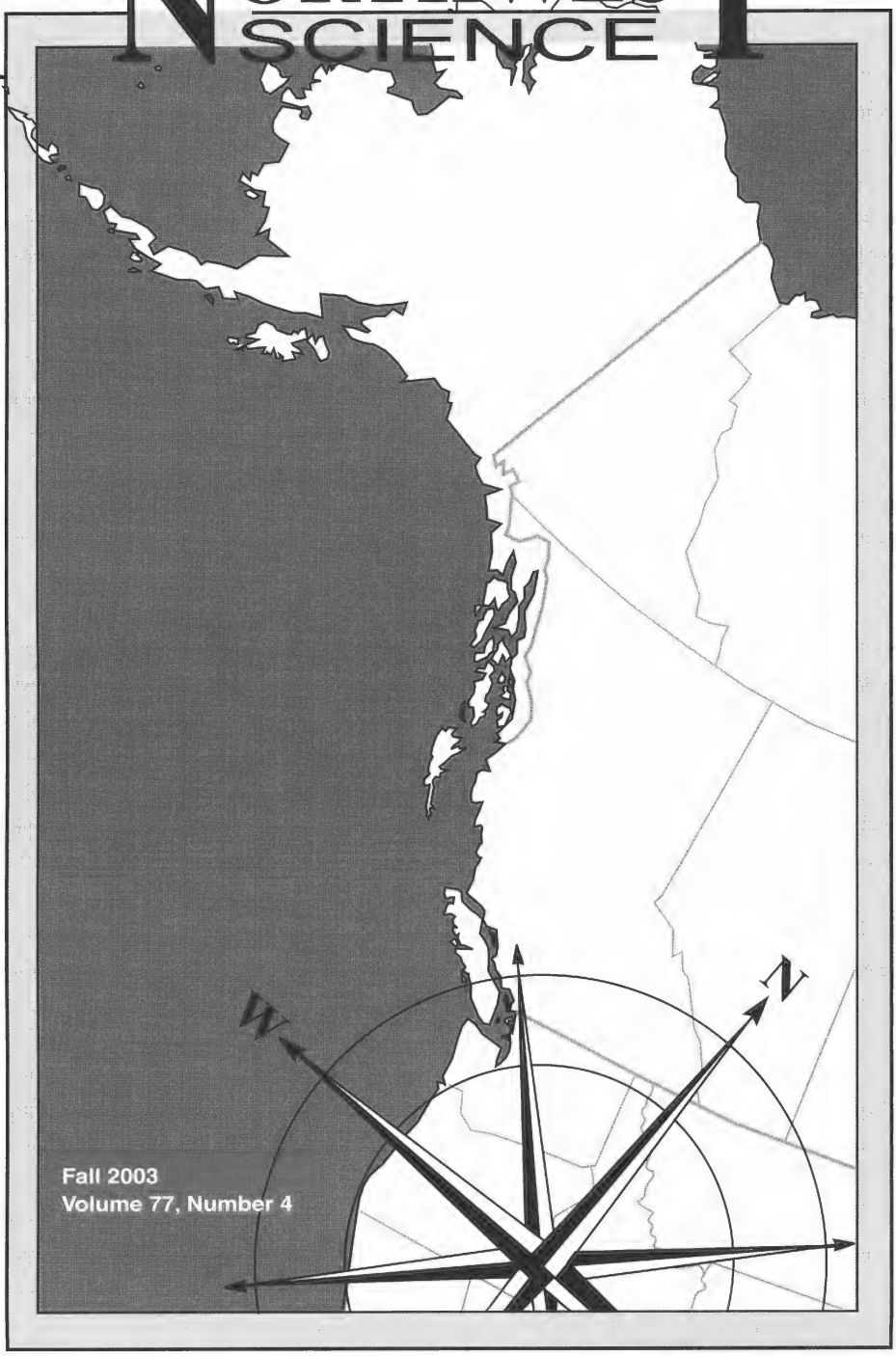
# NORTHWEST SCIENCE

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# Northwest Scientific Association

(Founded 1923)

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Fall 2003 Volume 77, Number 4

# NORTHWEST SCIENCE


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# Announcements

## Annual Meeting, Central Washington University, 24–27 March 2004

The 77th annual meeting of the Northwest Scientific Association will be hosted by Central Washington University in Ellensburg, Washington, from Wednesday, 24 March to Saturday, 27 March, 2004. Following a business meeting of the governing board on 24 March, scientific sessions will occur on the following two days with a variety of concurrent sessions and symposia including Natural Areas, Shrub-Steppe Ecosystems, and the Yakima River Basin. The Society for Northwestern Vertebrate Biology will also meet concurrently with the NWSA. Field trips will be offered to several sites in and around the Yakima River Basin on Saturday March 27.

Members and nonmembers are welcome at the annual meeting. Students are especially encouraged to attend and report the results of their research. Anyone interested in helping to organize or chair sessions should contact Karl Lillquist, Geography and Land Studies Department, Central Washington University, Ellensburg, Washington 98926; telephone 509-963-1184; fax 509-963-1047; e-mail: lillquis@cwu.edu. A call for abstracts and meeting registration will be mailed to all members of the Northwest Scientific Association.

## Call for Nominations

Nominations are invited for Honorary Life Member and Outstanding Scientist awards for the year 2004. Honorary Life Memberships are awarded to individuals who have worked for the continuing success of the Northwest Science Association with selfless enthusiasm and devotion. Outstanding Scientists are individuals who have made significant contributions to our understanding of basic or applied scientific issues that are especially relevant to northwestern North America. Recognition of Honorary Life Members and Outstanding Scientists is an important activity of the Northwest Science Association. Nominations for both awards should be sent to Paul Verrell (e-mail: verrell@wsu.edu) as soon as possible, and certainly not later than 1 January 2004.

## Northwest Scientific Association 2004 Student Research Grant Competition

The Northwest Scientific Association annually awards grants of up to $1000 to support student research in the pure and applied sciences. Applicants must be student members of NWSA (see inside front cover of *Northwest Science* for membership application information). Monies can only be used to support travel, equipment, and supplies for student research (proposals requesting salary support will not be considered).

Proposals should include (in the following order): 1) a cover page that provides the project title, name and address of the student applicant (including phone number and e-mail address), name of the major professor or advisor, and the dollar amount requested; 2) the body of the proposal, which provides an introduction (including the research question(s), objective(s) and significance), the literature background, the project methods (including experimental design, methodologies, appropriate

statistical analyses, and timeline), and expected results; 3) literature cited; 4) supplementary tables and figures; and 5) an itemized budget ($1000 maximum). The body of the proposal may not exceed four pages of double spaced text in 12-pt font with one inch margins (excluding title page, literature cited, supplementary tables and figures, and budget).

Four copies of the proposal must be received on or before 1 February 2004, and sent by surface mail to:

Dr. Steven A. Acker
Olympic National Park
500 East Park Avenue
Port Angeles, WA 98362

Grant winners will be announced at the NWSA annual meeting in Ellensburg, Washington, in March 2004. Grant recipients are required to present the results of their research at a future Northwest Scientific Association annual meeting. NWSA will waive page charges if grant recipients choose to publish their research in *Northwest Science* within four years of accepting their grant. Questions concerning grant application procedures should be directed to Dr. Steven A. Acker. His e-mail address is steve_acker@nps.gov.

## New Editor Needed

The Northwest Scientific Association is searching for a new editor to assume the duties after the NWSA annual meeting in Ellensburg, 24–27 March 2004. The term of the current editor of *Northwest Science* will expire in March 2004.

The person to become the next editor of *Northwest Science* should have good organizational skills, an ability to read and comment quickly on manuscripts that cover a variety of biological topics, diplomacy for dealing with authors, and an average of 8–10 hr per week available to oversee journal responsibilities. Much of the review process can be conducted in the evening. The workload is episodic. Previous editing experience is useful, but not essential. Past experiences as an author and as a reviewer are desirable. Institutional support, particularly for mailing and to supply assistants to help with the paperwork, makes this job much easier.

If you are interested in this position, please contact editor Rich Fonda by e-mail: fonda@biol.wwu.edu, or by phone: 360-650-6599.

**Philip W. Mote,**[1] JISAO/SMA Climate Impacts Group, Box 354235, University of Washington, Seattle, Washington 98195

# Trends in Temperature and Precipitation in the Pacific Northwest During the Twentieth Century

## Abstract

Documenting long-term trends or persistent shifts in temperature and precipitation is important for understanding present and future changes in flora and fauna. Carefully adjusted datasets for climate records in the USA and Canada are combined and used here to describe the spatial and seasonal variation in trends in the maritime, central, and Rocky Mountain climatic zones of the Pacific Northwest. Trends during the 20th century in annually averaged temperature (0.7°C–0.9°C) and precipitation (13%–38%) exceed the global averages. Largest warming rates occurred in the maritime zone and in winter and at lower elevations in all zones, and smallest warming rates occurred in autumn and in the Rockies. Largest increases in precipitation (upwards of 60% per century) were observed in the dry areas in northeast Washington and south central British Columbia. Increases in precipitation were largest in spring, but were also large in summer in the central and Rocky Mountain climatic zones. These trends have already had profound impacts on streamflow and on certain plant species in the region (Cayan et al. 2001), and other important impacts remain to be discovered. The warming observed in winter and spring can be attributed partially to climatic variations over the Pacific Ocean, and the buildup of greenhouse gases probably also plays an important role.

## Introduction

In the last ~150 yr, humans have enhanced the natural greenhouse effect of the atmosphere by increasing the quantities of key greenhouse gases. Carbon dioxide has increased 32% because of the burning of fossil fuels and deforestation, and methane has increased by 151% because of agriculture (chiefly cattle and rice paddies) and other human sources (Prentice et al. 2001). Other greenhouse gases have also increased, including $CF_4$, $C_2F_6$, and $SF_6$, whose human sources exceed natural sources by a factor of 1,000 or more, and some (e.g., the chlorofluorocarbons) that have no natural sources (Prather et al. 2001). In the global mean, $CO_2$ accounts for 60% of the radiative forcing by greenhouse gases, and $CH_4$ 20% (Ramaswamy et al. 2001).

During the 20th century, globally averaged surface temperature rose 0.6°±0.2°C, with most of the warming occurring in two intervals: between 1910 and 1945, and between 1976 and 2000 (Folland et al. 2001). Most evidence confirms that at least some of the rise in temperature can be attributed to the buildup of greenhouse gases (Mitchell et al., 2001). In addition to these instrumental records, evidence from a variety of natural systems also confirm recent warming: reductions in springtime northern hemisphere snow cover by 10%, in sea ice extent, and in length of most glaciers (Folland et al. 2001); changes in range of various flora and fauna, and timing of migration of diverse species (Walther et al. 2002). In western North America, warming has advanced the arrival of spring by 1-2 wk in the past 50 yr as indicated by various hydrologic and phenologic metrics (Cayan et al. 2001), and has reduced springtime snowpack in the Pacific Northwest (PNW) especially at elevations below about 1800 m (Mote 2003a).

Several studies (Easterling et al. 2000, Zhang et al. 2000, Folland et al. 2001) have displayed maps of trends in temperature and precipitation at the national or global scale, which show that temperature and precipitation have risen in the PNW during the 20th century. Southern British Columbia warmed substantially (roughly 0.5°-1.5°C), especially at night and in winter, and precipitation increased in all seasons in amounts between 5% and 35% (Zhang et al., 2000). It is difficult, however, to quantify regional or subregional trends from national maps like those shown by Zhang et al. (2000) especially when the distinction between adjacent colors is poor. Mote et al. (1999) presented maps and analysis for the U.S. part of the PNW, for which temperature rose 0.8°C and precipitation 14% during the 20th century.

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This article provides a regional focus for climatic trends in the PNW that may be useful for understanding other environmental changes and trends, augmenting the above-mentioned national- or global-scale studies. Also, this article emphasizes that the PNW is ecologically connected across the U.S.-Canada border. Mote (2003b) combined U.S. and Canadian data and examined the spatial and elevational dependence of the trends; this article uses more recent data for the USA, adds stations in western Montana, provides a basis for combining the datasets, and examines seasonal and interannual characteristics of the variability and trends.

## Data and Methods

For this study I circumscribe the Pacific Northwest by the Continental Divide, the 111° meridian, and the latitudes 42° and 55°. This definition encompasses Washington, Oregon, and Idaho in their entirety, southern and central British Columbia, and a portion of western Montana. I use station data compiled and adjusted separately by the U.S and Canadian climate centers.

For the Canadian portion of the study area, I use the Historical Canadian Climate Database (HCCD) (Vincent and Gullett 1999), which has 32 stations with temperature records and 81 stations with precipitation records. For the U.S. portion of the study area I use the Historical Climate Network (USHCN) (Karl et al. 1990), which has 122 stations with temperature records and 84 stations with precipitation records. The period of record with best coverage (Figure 1) is roughly 1925-2000 for USHCN and 1950-1995 for HCCD, although for both datasets a majority of stations have periods of record beginning by 1920. Many stations have gaps in their precipitation records as indicated by the fluctuating totals. In this paper I will compare trends at different locations over the period of record 1930-1995 and areally combined trends over different periods of record; results (especially for temperature) are relatively insensitive to period of record.

Weather stations were not originally intended for monitoring long-term trends, and therefore these datasets have been adjusted to account for factors that can influence measurements, including changes in instrument, changes in observing practices, and relocation of the station. For example, weather observations at Vancouver, Washington (Figure 2) have a varied history. This station has the earliest measurements in the USHCN database for the Northwest. Measurements began in December 1849 at Fort Vancouver, were discontinued in 1868, resumed for a few years around 1890, resumed again in 1895, and continued without major interruption until 1966. In mid-1966

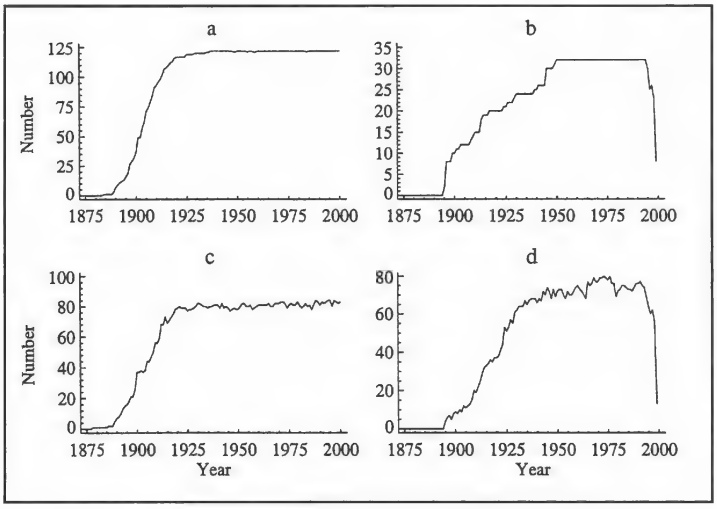


Figure 1. Number of stations reporting annual mean temperature (a, b) or precipitation (c, d) in each year for the USHCN dataset (a, c) and the HCCD dataset (b, d).

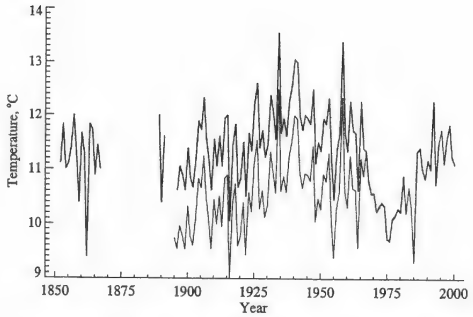


Figure 2. Annual mean temperature at Vancouver, Washington, showing the difference between unadjusted (upper) and adjusted (lower, shorter) station records in the USHCN dataset. In 1966 the station was moved about 4 km, and the new site had a lower annual mean temperature; the earlier record was adjusted to reflect this change. After 1966 the two time series are nearly identical. Adjustments at other stations were almost all smaller than those shown here.

the station was moved 4.6 km northeast, and at the new location, the mean temperature was approximately 1°C lower, so that the earlier part of the data record was adjusted downward to be consistent. (Adjustments related to station changes are always applied to the earlier part of the record so that new observations can be added with no further adjustments.) The measurements before 1888 were not performed with a properly sheltered, min-max thermometer and are excluded. Differences between adjusted and unadjusted records were typically much smaller than this example, and few had such dramatic step changes.

One concern about combining the USHCN and HCCD databases is that somewhat different procedures were used by the two national climate centers in processing and adjusting station data. An indication of consistency between datasets can be derived by comparing proximate stations, like Porthill, Idaho, and Creston, British Columbia, which are 10 km apart (Porthill is 56m lower in elevation). Their annual temperature records (Figure 3) are correlated at 0.94 and have nearly identical trends (1.3° and 1.5°C). The difference in means (0.4°C) is not statistically significant. From this limited comparison, combining the datasets seems reasonable.

To examine the temporal (seasonal, interannual, and longer-term fluctuations) characteristics of

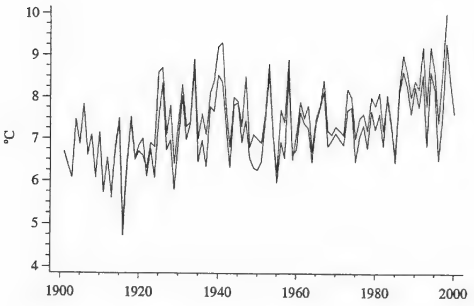


Figure 3. Comparison of annual mean temperature at Porthill, Idaho (lower), period of record 1901-2000 from the USHCN dataset, and Creston, British Columbia (upper), period of record 1913-1998 from the HCCD dataset. The two stations are about 10 km apart and both records have been adjusted to remove various time-dependent biases.

the temperature variations, it is necessary to combine or aggregate the station data in some way. Various approaches have been used in previous studies, including averaging in latitude-longitude bins (Easterling et al. 2000, Zhang et al. 2000), averaging in climate divisions and then weighting by area of climate division to form a regional average (Mote et al. 1999), or thinning the stations to a more nearly uniform density (Frich et al. 2002). In this study, following Mote (2003b), I divide the Northwest into three broad climatic and ecological zones: the maritime zone, encompassing stations west of the crest of the Cascade mountains and those in British Columbia lying in or west of the coastal mountains; the Rockies, encompassing stations in north-central and eastern British Columbia, Montana, and most of Idaho; and the central zone, encompassing stations in eastern Washington, eastern Oregon, the Snake River Plain, a few other moderate-elevation (<1160m) stations in western Idaho, and south-central British Columbia south of Kamloops. Monthly mean temperatures in each zone are calculated using only those stations with nearly continuous records from 1920 to 1999, to ensure that no spurious trend will arise as a result of changes in the population of stations used from year to year. Values before 1920 are calculated from stations as available and are plotted but not included in the analysis.

To examine connections between PNW climate variability and North Pacific climatic variations,

I perform regression analysis of these Northwest climate data using a time series of the North Pacific Index (Trenberth and Hurrell, 1994). The North Pacific Index (NPI) is defined as the mean sea level pressure over the region 30°-60°N, 160°E-140°W, and I use here the NPI value corresponding to the season being analyzed. Regression analysis (von Storch and Zwiers, 2001) identifies linear relationships between variables, much like correlation analysis but with the dimensions of the original variable (°C for temperature, cm for precipitation) preserved. Analyses are performed over the period 1920-2000, and statistical significance ($P<0.05$) is determined using the method of Bretherton et al. (1999) to estimate number of degrees of freedom, accounting for the structure of the serial autocorrelation function.

## Results

### Temperature Trends

As a first look at temperature trends, I plot at each station the 1930-1995 trend using linear least squares fit (Figure 4). At the vast majority of sta-

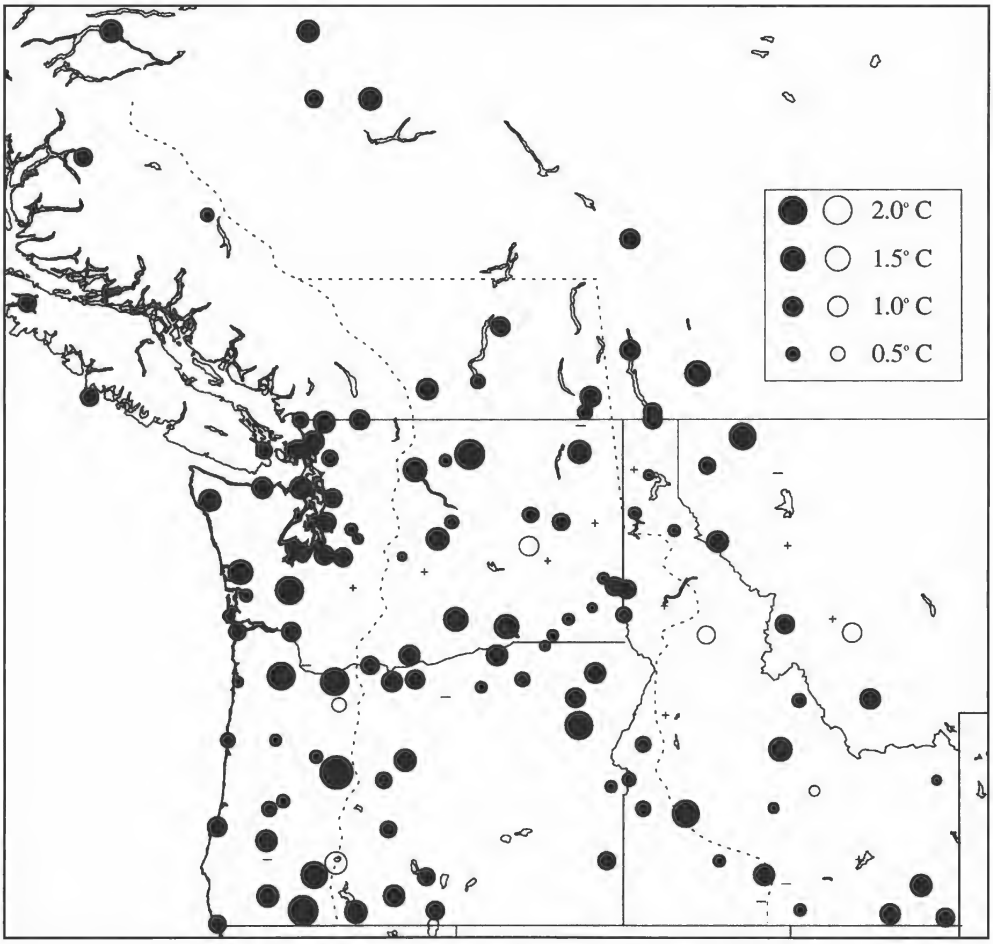


Figure 4. Linear trends in annual temperature at each station. Trends are calculated for the period from 1930 to the end of the record (must be at least 1995) and scaled to give temperature change per 100 yr. Positive trends are shown as filled circles and negative trends as open circles, and the area of the circle is proportional to the magnitude of the trend as indicated in the legend. But trends between 0 and 0.25° C are marked with a '+' and trends between –0.25 and 0° C are marked with a '–'. Dotted curves show the boundaries of climatic zones used in Figures 6 and 9.

tions in the Northwest, the temperature trends have been positive. In each of the four states, but not in British Columbia, trends have been negative at a handful of stations. Stations in and near urban and rural areas have similar trends, and in each state the largest warming trend is in a rural area or small town.

To indicate how the trends depend on the period of record, Figure 5 shows quantile distributions of total change from year indicated to the end of the record. For no choice of starting point are more than 10% of trends negative. A starting point of 1925 yields the largest fraction of negative trends, the smallest mean changes, and the smallest trends. For starting years from 1925 to about 1945, both the mode and the mean increase gradually from about 0.5°C to 1°C.

From the monthly mean temperatures calculated for each climatic, time series and linear trends

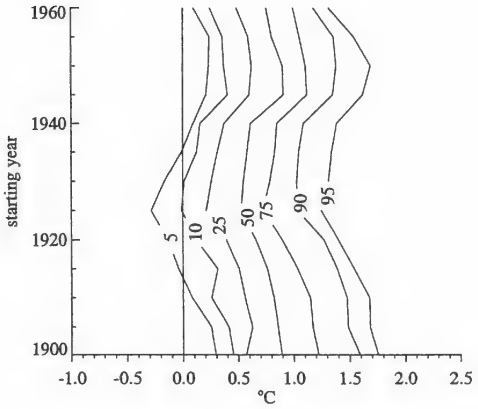


Figure 5. Quantiles (e.g., 50 = 50%) in the distribution of linear trends, evaluated for each starting year at 5-yr intervals as total changes from then to the ending year (required to be at least 1996). The number of stations included in the analysis increases with time as indicated in Figure 1.

in monthly, seasonal, and annual temperatures are calculated; Figure 6 shows the results for seasonal and annual temperatures in each climatic zone. The trend in annual average temperature decreases from the maritime zone (0.91°C) to the central zone (0.83°C) to the Rockies (0.73°C), and in all zones the trend is large and somewhat greater than the global average trend over the 20th century (0.6°C), but is only significant in the central zone. In all three zones, trends are largest in winter (January-February-March) and in all but the maritime zone trends in other seasons are small. Trends are smallest in autumn (October-November-December) in all three zones.

Interannual variations in the region's climate are coherent: The three time series of annual temperature (top row) are significantly correlated (0.90 for maritime and Rockies, 0.85 for maritime and central, 0.96 for central and Rockies). The extreme years tend to be similar among the zones: 1955 and 1985 are among the coldest in all three zones, and 1934 and 1992 are among the warmest. The extreme years are often determined by only one season: 1985 had an unusually cold autumn, especially in the Central zone, and 1934 was an unusually warm winter in all zones. In all zones the 1990s were the warmest decade, warmer than any other decade by about 0.4°C-0.5°C; these differences are statistically significant for the maritime and central zones.

Climatic patterns over the Pacific Ocean play an important role in year-to-year climatic variations, and hence potentially influence long-term trends as well. As described earlier, I regressed each of the time series of temperature shown in Figure 6 on the north Pacific index (NPI); the linear trend in the regressed values is then expressed as a fraction of the trend in the data (NPI fraction of trend). Table 1 shows the correlation coefficient and NPI fraction of trend for the annual mean and the winter season, when correlations and trends are significant. The NPI explains 30-40% of the

TABLE 1. Correlations between North Pacific Index (NPI) and temperature, and fraction of the trend attributable to NPI, for the annual mean and winter. In other seasons either the correlation or the trend fails a significance test.

| | Maritime | | Central | | Rockies | |
|---|---|---|---|---|---|---|
| | Correlation | Fraction | Correlation | Fraction | Correlation | Fraction |
| Annual | -0.69 | 11% | -0.52 | 11% | -0.55 | 12% |
| JFM | -0.79 | 41% | -0.63 | 36% | -0.65 | 32% |

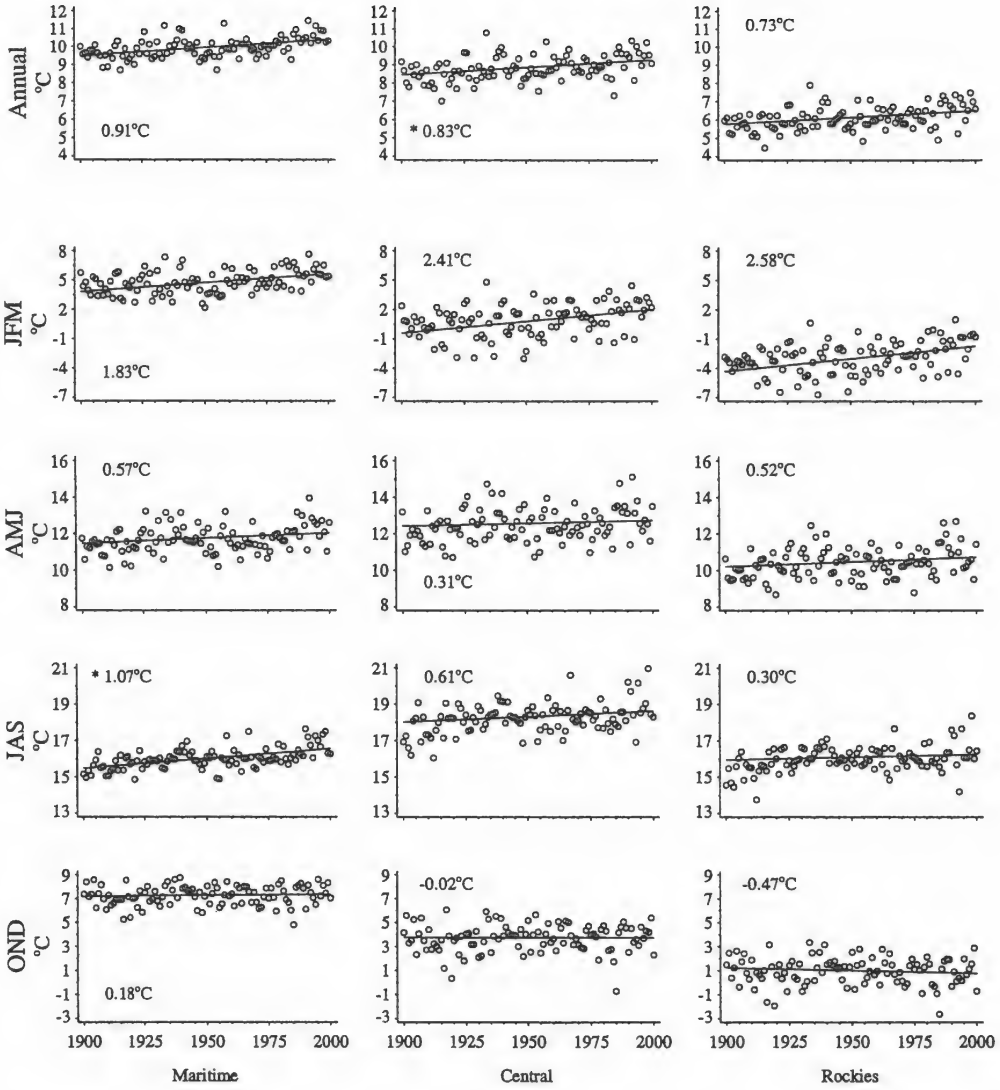


Figure 6. Temperature, averaged over all stations in each of three climate zones (columns, as indicated) for annual mean (top row) and each of four seasons as indicated. The linear trend over the 1920-2000 period, expressed in degrees per century, is indicated in each panel and marked by a '*' if significant at $P < 0.05$. In each row the scale on the ordinate is the same for all three zones. Note that trends in each climate zone are largest in winter (JFM).

large winter trends but only a small portion of the trends in annual mean. For spring, correlations are significant (ranging from –0.35 to –0.45), but trends are not; in other seasons, correlations are not significant.

## Precipitation Trends

Although total precipitation at a given location helps determine which flora will be found there, relative (percentage) changes in precipitation are often more relevant for changes in biological pro-

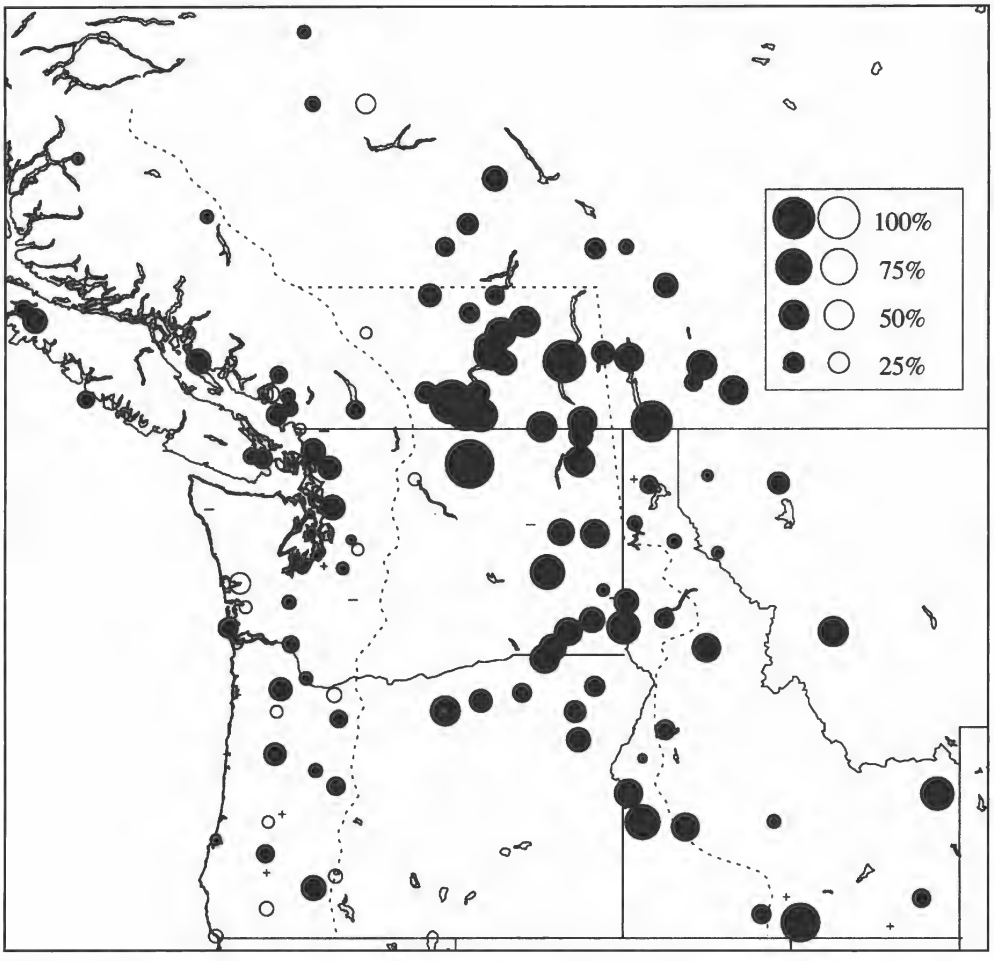


Figure 7. As in Figure 4 but for relative trends in precipitation, calculated for each station as a percentage of the value in 1930. The largest trend, at Conconully, Wash., is 135% per century. Trends between 0 and 5% are marked with a '+' and trends between –5 and 0% are marked with a '–'.

ductivity or functioning. An additional 10 cm of precipitation may be functionally irrelevant at a wet coastal location where 10 cm amounts to 4% of the annual total, but 10 cm may be significant at a dry location with annual precipitation of 20 cm. In this paper I present both absolute and relative trends, but emphasize relative trends.

Like the trends in temperature, trends in precipitation (Figure 7) are overwhelmingly positive over the period 1930-1995. In the maritime zone, most stations show modest relative increases, but some showing decreases are interspersed. Other zones have almost no stations with negative trends. The tenth percentile, median, and ninetieth percentile are –1%, 22%, and 58%, and none of the negative trends is statistically significant.

The most intriguing feature in Figure 7 is the collection of stations in eastern Washington and southeastern BC where precipitation rose significantly, many >60% per century. At Conconully, Washington, annual precipitation rose 135%. At most of these stations, precipitation rose the most during the spring and early summer (April-July).

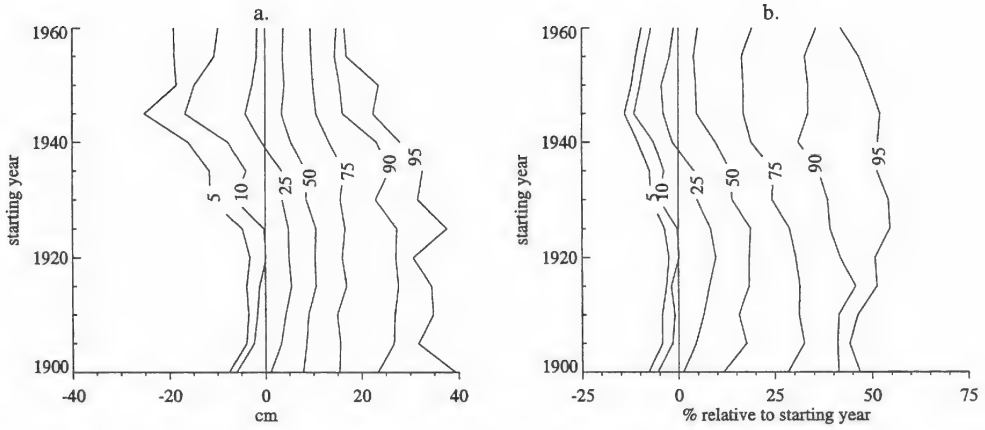


Figure 8. As in Figure 5, but for precipitation expressed as both absolute trends (left) and relative trends (right) over the given period of record.

As with temperature, I plot quantiles of precipitation changes as a function of starting year (Figure 8). The shape of the distribution is somewhat skewed, with steeper changes below the mode than above it, and changes little from 1900 to 1925. In contrast to the monotonic increases in temperature seen in Figure 5, trends in precipitation taken from starting points later in the record (e.g., after 1930) are more likely to be negative because precipitation fluctuates more on interdecadal timescales. Regardless of starting year, the median change is ~5-10 cm. Total relative change is most likely to be in the range of 10-30% before about 1935. Most of the increase in precipitation over the 20th century occurred before 1945, and trends over the second half of the century are somewhat smaller.

Important differences are seen when precipitation variability and trends are examined by season and by zone (Figure 9). As expected from Figure 7, the largest relative trend (38%) is in the central zone, but statistically significant increases occur in spring in the other two zones. Interannual variations in precipitation are significantly correlated among the regions (0.70 between maritime and central, 0.65 between maritime and Rockies, and 0.82 between central and Rockies). The wettest year (1996) was wettest in all three zones. Disparity was greater among the driest years, though the combination of the dry fall in 1976 (the driest in each zone) and fairly dry winter in 1977 in the central zone and the Rockies made the 1976-77 October-March period the driest in the 20th century.

The seasonality of precipitation trends has some interesting features. In all three zones absolute trends are largest and statistically significant in spring, and in the maritime zone the relative trends are largest in spring, too. For the central zone, summertime precipitation increased by about 70% but this increase is not statistically significant. As with temperature, trends are largest in autumn.

Correlations between NPI and precipitation are $\leq 0.26$, and in only one case (wintertime trend in the central climatic zone) statistically significant. The variability and trends in precipitation are not well explained by NPI.

## Discussion

Global temperature and precipitation have increased (Folland et al. 2001), and PNW temperature and precipitation have increased more than the global averages (Figures 4, 6, 7, 9). The long-term fluctuations in temperature are fairly well represented by linear trends, but the long-term fluctuations in precipitation are somewhat more cyclical, partly owing to the Pacific Decadal Oscillation (Mantua et al. 1997). The changes are sufficiently widespread and coherent to rule out factors unrelated to large-scale climate, like land-use change. These trends are undoubtedly real, and the warming is large enough to have signifi-

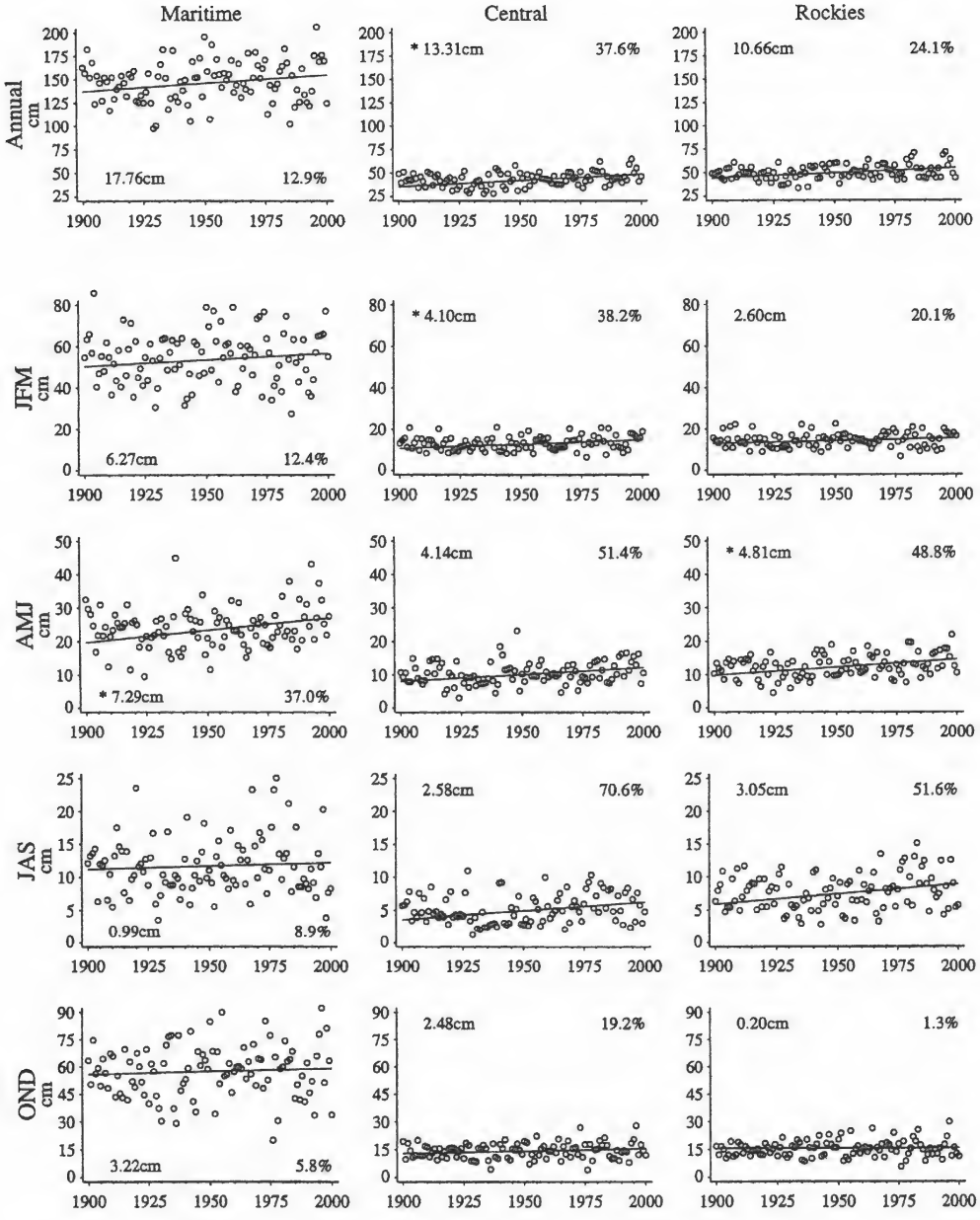


Figure 9. As in Figure 6 but for precipitation. Numerical values of absolute and relative trends are shown in each panel.

cant impacts on the hydrology and ecosystems of the region (Cayan et al. 2001). Several aspects of the trends bear further discussion.

One must use caution in interpreting trends at individual stations owing to possible non-climatic factors. Note, for example, the string of stations just inland of the Oregon coast with trends of alternating sign (Figure 7). Where groups of nearby stations show similar trends, the trends likely reflect genuine climatic trends. In one case, an unusual piece of evidence provides independent confirmation. Crater Lake, Oregon, lies on the crest of the Cascades near Prospect, Oregon (the large positive trend near the California border). The long-term trend in precipitation at Crater Lake was examined by Peterson et al. (1999), who showed that a reconstruction of changes in lake level derived from estimates of precipitation from tree-ring data approximately matches the observed changes in lake level, which dropped ~2 m during the 20th century.

The dependence of these trends on elevation was examined by Mote (2003b). A linear fit of trend to elevation revealed a general decline in both temperature and precipitation trends (both absolute and relative) with elevation, in contrast to expectations from experiments with global (Fyfe and Flato 1999) and regional (Giorgi et al. 1997) climate models. In modeling experiments, the snow-albedo feedback, in which a slight warming near the snowline melts snow and allows the surface to absorb more solar radiation, drives substantial warming in winter and spring, and this warming is enhanced at higher altitudes. Two possible reasons for this discrepancy are 1) since the climate stations are almost all in valley bottoms, the elevational dependence calculated from them does not reflect the elevational dependence in mountainous terrain; 2) other mechanisms (e.g., changes in cloudiness) may overwhelm the snow-albedo feedback. All three climatic zones showed largest trends in winter, consistent with a snow-albedo feedback mechanism, but since the maritime stations rarely experience snow their large trends must be influenced by other factors.

Determining the causes of these trends is difficult, although some possible causes can easily be ruled out. The warming trends are clearly not a spurious by-product of urbanization, since trends in urban areas are no larger than those in rural areas. Although attribution of causes of temperature trends is possible on the scale of continents (Stott and Tett, 1998), it is not yet possible for a region the size of the Pacific Northwest, in part because changes in atmospheric circulation can make one region warm and another cool without changing the global average. Circulation changes, for example associated with the Pacific Decadal Oscillation or El Niño, were represented here by the North Pacific Index and may partly explain the trends in temperature but not precipitation. The positive trends shown here for both temperature and precipitation are roughly consistent with changes simulated by climate models for the 20th century using observed changes in carbon dioxide (Mote et al. 2003).

The observed warming is confirmed by various hydrological and phenological signals (Cayan et al. 2001). Conversely, the changes in temperature have already had an observable effect on key parts of various ecosystems (Cayan et al. 2001, Walther et al. 2002). But one of the most striking observations presented here is of the large increase in precipitation, especially in spring and summer, in the inland Northwest. These increases are especially large in eastern Washington and southern British Columbia, but I know of no evidence that vegetation has responded to these increases in precipitation.

## Acknowledgements

Kelly Redmond, Nathan Mantua, David L. Peterson, and John M. Wallace provided helpful suggestions for an earlier draft of this manuscript. This is JISAO contribution number 966; this publication is supported by a grant to the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement no. NA17RJ1232.

## Literature Cited


Bretherton, C. S., M. Widmann, V. P. Dymnikov, J. M. Wallace, and I. Bladé. 1999. Effective number of degrees of freedom of a spatial field. Journal of Climate 12:1990-2009.

Cayan, D. R., S. A. Kammerdiener, M. D. Dettinger, J. M. Caprio, and D. H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 82:399-415.

Easterling, D. R., T. R. Karl, K. P. Gallo, D. A. Robinson, K. E. Trenberth, and A. Dai. 2000. Observed climate variability and change of relevance to the biosphere. Journal of Geophysical Research 105:20,101-20,114.

Folland, C. K., T. Karl, J. Christy, R. Clarke, G. Gruza, J. Jouzel, M. Mann, J. Oerlemans, M. Salinger, and S.-W. Wang. 2001. Pages 99-182 *In* J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (editors), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Frich, P., L. V. Alexander, P. Della-Marta, B. Gleason, M. Haylock, A. M. G. Klein Tank, and T. Peterson. 2002. Observed coherent changes in climatic extremes during the second half of the twentieth century. Climate Research 19:193-212.

Fyfe, J. C., and G. M. Flato. 1999. Enhanced climate change and its detection over the Rocky Mountains. Journal of Climate 12:230-243.

Giorgi, F., J. W. Hurrel, M. R. Marinucci, and M. Beniston. 1997. Elevation signal in surface climate change: A model study. Journal of Climate 10:288-296.

Karl, T. R., C. N. Williams Jr, F. T. Quinlan, and T. A. Boden. 1990. United States Historical Climatology Network (HCN) serial temperature and precipitation data, Environmental Science Division, Publication No. 304, Carbon Dioxide Information and Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079.

Mitchell, J. F. B., D. Karoly, G. Hegerl, F. Zwiers, M. Allen, and J. Marengo. 2001. Detection of climate change and attribution of causes. Pages 695-738 *In* J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (editors), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Mote, P. W. 2003a. Trends in snow water equivalent in the Pacific Northwest and their climatic causes. Geophysical Research Letters 30:doi 10.1029/2003GL017258.

Mote, P. W. 2003b. How and why is Northwest climate changing? *In* D. L. Peterson and J. L. Innes (editors), Climate Change, Carbon, and Forestry in Northwestern North America. USDA Forest Service General Technical Report GTR-, Pacific Northwest Research Station, Portland Oregon. (*in press*).

Mote, P. W., D. Canning, D. Fluharty, R. Francis, J. Franklin, A. Hamlet, M. Hershman, M. Holmbeg, K. Ideker, W. Keeton, D. Lettenmaier, R. Leung, N. Mantua, E. Miles, B. Noble, H. Parandvash, D. W. Peterson, A. Snover, and S. Willard. 1999. Impacts of Climate Variability and Change: Pacific Northwest. University of Washington Climate Impacts Group. Available online at http://jisao.washington.edu/PNWimpacts/Publications/Pub120a.htm.

Mote, P. W., E. A. Parson, A. F. Hamlet, W. S. Keeton, D. P. Lettenmaier, N. J. Mantua, E. L. Miles, D. W. Peterson, D. L. Peterson, R. Slaughter, and A. K. Snover. 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. Climatic Change. (*in press*).

Peterson, D. L., D. G. Silsbee, and K. T. Redmond. 1999. Detecting long-term hydrological patterns at Crater Lake, Oregon. Northwest Science 73:121-130.

Prather, M., D. Ehhalt, F. Dentener, R. Derwent, E. Glugokencky, E. Holland, I. Isaksen, J. Katima, V. Kirchhoff, P. Matson, P. Midgley, and M. Wang. 2001. Atmospheric chemistry and greenhouse gases. Pages 239-288 *In* J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (editors), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Prentice, I. C., G. Farquhar, M. Fasham, M. Goulden, M. Heimann, V. Jaramillo, H. Kheshgi, C. Le Quéré, R. Scholes, and D. Wallace. 2001. The carbon cycle and atmospheric carbon dioxide. Pages 183-238 *In* J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (editors), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Ramaswamy, V., O. Boucher, J. Haigh, D. Hauglustaine, J. Haywood, G. Myhre, T. Nakajima, G.Y. Shi, and S. Solomon. 2001. Radiative forcing of climate change, Pages 349-416 *In* J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson (editors), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Stott, P. A., and S. F. B. Tett. 1998. Scale-dependent detection of climate change. Journal of Climate 11:3282-3294.

Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9:303-319.

Vincent, L. A., and D. W. Gullett. 1999. Canadian historical and homogeneous temperature datasets for climate change analysis. International Journal of Climatology 19:1375-1388.

Von Storch, H., and F. Zwiers. 2001. Statistical Analysis in Climate Prediction. Cambridge University Press, Cambridge, United Kingdom.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Zhang, X., L.A. Vincent, W.D. Hogg, and A. Niitsoo. 2000. Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38:395-429.

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# Forest Colonization of Puget Lowland Grasslands at Fort Lewis, Washington

## Abstract

As a result of fire exclusion since the mid-19th century, Douglas-fir has been invading the grasslands of the southern Puget Lowland, Washington, converting them to colonization forests. We studied a chronosequence of these forests, including some that received periodic commercial thinnings, at Fort Lewis Military Reservation to elucidate successional patterns and changes in ecosystem properties associated with tree invasion. In unmanaged colonization forests (ages 27-120 yr), overstory cover and tree density remained constant after 27 yr, while basal area increased. Shrub cover increased with age and, after an initial decrease compared to grasslands, ground cover also increased. Shrub species richness increased over time, while ground-layer richness was much less than in grasslands, and there was a rapid shift from grassland to forest floras. Dead wood (snags and logs) accumulated gradually. The only change in soil properties was lower A-horizon nitrogen. In managed colonization forests (ages 55-91 yr), tree density, overstory cover, and total log length decreased over time, but shrub cover and A-horizon cation-exchange capacity, carbon, and nitrogen increased over time. Although structural and floristic conversion of grassland to forest requires < 30 yr, soil changes are much more gradual, such that the soils underlying colonization forests up to 400 yr old are still classified as grassland soils. Higher tree densities in colonization forests compared to the pre-settlement forests of Fort Lewis mean an increased risk of crown fires during droughts. Even with active management, colonization forests will require many decades to provide northern spotted owl habitat because they lack shade-tolerant conifers and large live trees, snags, and logs.

## Introduction

Grassland ecosystems in many regions of the world were once maintained by natural or anthropogenic fire in climates that could support forests or woodlands. However, during the 20th century, human influences have caused drastic reductions in grassland fire frequency. As a result of fire exclusion, trees and shrubs are invading many grasslands (Archer 2003), producing multiple changes in ecosystem properties. Changes in vegetation include dominance by woody as opposed to herbaceous species (Archer 1995, Arabas 2000, Miller and Tausch 2001, Briggs et al. 2002), decreased herbaceous species diversity (Archer 1995, Miller and Tausch 2001), and reduced grass, forb, and sometimes shrub biomass (Bailey and Wroe 1974, Archer 1995, Miller and Tausch 2001, Briggs et al. 2002). Dead wood accumulates also, particularly once woody plant mortality commences. Changes in soils include greater O-horizon and mineral soil depth (Barton and Wallenstein 1997), lower soil pH (Barton and Wallenstein 1997), and either higher or lower soil carbon, nitrogen, and other nutrients (Archer 1995, Miller and Wigand 1994, Barton and Wallenstein 1997, Gill and Burke 1999). These soil changes suggest the potential for altered site productivity, though no study has specifically examined this possibility. Nor is it clear how long it might take for soil properties to change enough for grassland soils to be reclassified as woodland or forest soils.

Woody plant invasion of grasslands is usually a patchy process (Grimm 1983, Archer et al. 1988, Knight et al. 1994, Barton and Wallenstein 1997), so the resulting changes in vegetation and soil properties can be spatially complex (Miller and Wigand 1994, Archer 1995, Barton and Wallenstein 1997). In addition, alterations in the distribution and amount of live and dead fuels associated with invasion affect wildfire risk (Miller and Tausch 2001, Peterson and Hammer 2001).

Tree invasion of grasslands is ongoing in the southern Puget Lowland and the San Juan Islands of western Washington. An estimated 60,500 ha of grasslands existed in the southern Puget Lowland prior to settlement by European-Americans (Crawford and Hall 1997), and substantial portions of the San Juan Islands were also grassland then (Peterson and Hammer 2001). Fossil pollen records indicate that these grasslands developed during a

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period of warmer, drier climate 7,000 to 10,000 yr ago (Hibbert 1979, Whitlock 1992). As the climate became cooler and wetter, the grasslands persisted because of periodic fires set by Native Americans to perpetuate important food plants, such as camas (*Camassia quamash*) (Perdue 1997). Following settlement in the mid-19th century, grassland fires largely ceased, and Douglas-fir (*Pseudotsuga menziesii*) began invading the grasslands, a process that continues today (Kruckeberg 1991). The early stages of invasion occur in a patchy fashion, with founder trees serving as nuclei for clumps of trees that gradually expand and coalesce to form colonization forests (Giles 1970). The result, as Peterson and Hammer (2001) observed on Orcas Island, Washington, is mosaics of unevenaged colonization forest and remnant prairie patches. Compared to adjacent areas that have been forested for much of the Holocene, colonization forests have few shade-tolerant conifers, possess less-well-developed shrub layers, and lack legacy (large live trees, snags, and logs left over from previous forests occupying the same sites) (Ahrens 1998a, 1998b).

Fort Lewis Military Reservation, a U.S. Army installation located between Tacoma and Olympia, is a good site to study colonization forests, for several reasons. First, forest invasion of prairies is well documented there. Large areas of present-day conifer forest at Fort Lewis are mapped by NRCS soil surveys as growing on grassland soils (Anderson et al. 1955, Pringle 1990). In addition, a comparison of current Fort Lewis vegetation with vegetation recorded by mid-19th century land surveys indicates that 6,600 ha of former prairie are now occupied by conifer forest (Public Forestry Foundation 1996). A second reason is that the installation possesses most of the extant grasslands and colonization forests in the southern Puget Lowland. Elsewhere in the region, grasslands and colonization forests have been heavily fragmented by agriculture and urban development. A third reason is that the majority of Fort Lewis' colonization forests are subject to a consistent regime of silvicultural manipulation, primarily light thinnings (15-20% of basal area removed) at roughly 10-yr intervals, but some have received no timber harvest. Thus, Fort Lewis offers the opportunity to assess the influence of active forest management on the timing and duration of ecosystem changes during tree invasion. For example, does periodic logging differentially affect dead wood accumulation or soil properties in managed vs. unmanaged colonization forests? A final reason is that Fort Lewis' forests are critical habitat for the northern spotted owl (*Strix occidentalis caurina*) and must be managed in a manner that will hasten the development of late-successional stand structures (e.g., multiple canopy levels and large trees, snags, and logs) that benefit the owl (Public Forestry Foundation 1996). What contribution, if any, can colonization forests make to owl habitat?

The purpose of this study was to describe successional patterns and associated changes in ecosystem properties that have occurred as a result of Douglas-fir invasion of Puget Lowland grasslands following fire exclusion. Specifically, we examined temporal changes in tree size and density, vegetation layering, species diversity, dead wood and litter accumulation, and soil chemical and physical properties. We compared these changes between forests that had received commercial timber harvest and forests that had not been harvested, and we considered the consequences of these changes for forest management, including timber harvest, spotted owl habitat, wildfire risk, and site productivity.

## Methods

### Chronosequence Approach

Historical records are sketchy, and the oldest aerial photos of Fort Lewis were taken in 1942. Therefore, our primary tool to assess changes over time during tree invasion was to examine vegetation structure and soil characteristics in a chronosequence of sites ranging from open grasslands to 130-yr-old colonization forests. Such space-for-time substitution assumes that the same ecological processes are at work in the past as in the present. Specifically, we assumed that during the past 130 yr, (1) the structure and composition of grassland vegetation at the start of colonization have remained the same, and (2) the direction and magnitude of ecosystem changes during tree invasion have remained the same, regardless of when invasion began.

Available evidence suggests that neither of these assumptions is correct. The starting point of tree invasion has changed in recent years from grasslands dominated by the native perennial bunchgrass, Roemer's fescue (*Festuca roemerii*), to grasslands infested with exotic species, such as the leguminous shrub, Scot's broom (*Cytisus*

*scoparius*), and sod-forming grasses, especially colonial bentgrass (*Agrostis tenuis*). Scot's broom forms dense, monospecific shrubfields, slowing or preventing forest invasion by shading conifer seedlings. Sod-forming grasses outcompete and eventually exclude Roemer's fescue.

The processes potentially affecting tree invasion have also changed over time. Most of Fort Lewis' grasslands were grazed from the mid-19th century until 1975. In addition, military training has varied in type and intensity since Fort Lewis was established in 1917. For example, tracked-vehicle training on grasslands increased substantially between 1995 and 2001, compared to previous years. The long-term effect of this type of training is a shift in grassland plant species composition toward more dominance by exotics (U.S. Army Corps of Engineers 1994). In addition, in high-use military areas, such as bivouac sites, much of the shrub and ground cover is eliminated and tree establishment is inhibited.

The likely consequence of violations of our two assumptions is an increase in within- and between-site variance of colonization forest structure, making statistical detection of temporal change more difficult.

## Study Sites and Sample Plots

We used soil and forest data layers from the Fort Lewis geographic information systems (GIS) lab to compile a map of colonization forests on the installation. The soil layer was derived from detailed soil surveys (Andersen et al. 1955, Pringle 1990), which list the Spanaway, Fitch, and Nisqually series as having formed with grassland vegetation. These soils are gravelly sandy loams with organic matter-rich A horizons, 30-40 cm thick. The forest layer classified stands into age classes (10-yr intervals), which we considered to be rough estimates. Any forests occurring on grassland soils were considered to be colonization forests. Using the forest GIS layer and timber-sale records from the Fort Lewis Forestry Program, we categorized colonization forests according to age class and management status (i.e., managed for timber harvest vs. unmanaged).

There was an insufficient number of stands ($n < 3$) in most of the unmanaged age classes to use stands as statistical replicates. Instead, individual plots, randomly located across the total mapped area of each age class, served as replicates for both unmanaged and managed forests. This experimental design permitted inferences to be made about individual age classes, but not individual stands, of colonization forest at Fort Lewis.

Managed forests < 50 yr of age do not exist at Fort Lewis because they contain too few commercial-sized trees to justify timber harvest, so that the youngest managed age class in this study was 51-60 yr. Also, for logistical reasons, we chose to sample from only four out of the six available age classes of unmanaged forests.

Sample size was 10 plots in each age class/management status combination ≥ 50 yr of age (except n = 8 in 71- to 80-yr-old, managed forests). Since our field observations indicated young colonization forests have greater spatial variability in stand structure than do older colonization forests, we increased sample sizes in age classes < 50 yr old (Table 1). We randomly allocated additional plots, representing year zero of colonization, across the GIS-mapped grasslands at Fort Lewis.

Each sample plot consisted of of two nested, circular plots of 1000 $m^2$ (17.84-m radius) and 500 $m^2$ (12.62-m radius) area. Four 100 $m^2$ (5.64-m radius) plots were equally spaced around the edge of the 1000 $m^2$ plot, and a fifth 100 $m^2$ plot was located at the center of the 1000 $m^2$ plot. A 20 $m^2$ plot and a 2 $m^2$ plot were nested within each

TABLE 1. Available area on Fort Lewis, number of replicate plots, and plot ages (mean ± 1 SE) for unmanaged and managed forest age classes. Age 0 yr represents grassland plots.

| Age Class (yr) | Area (ha) | No. Plots | Plot Age (yr) |
|---|---|---|---|
| | Unmanaged Forests | | |
| 0 | ~6,500 | 10 | 0 |
| 11-20 | 85 | 25[1] | 27 ± 2 |
| 21-30 | 199 | 20[2] | 32 ± 1 |
| 31-40 | 58 | 15 | 47 ± 5 |
| 51-60 | 56 | 10 | 56 ± 5 |
| 71-80 | 131 | 10 | 63 ± 5 |
| 101-110 | 42 | 10 | 92 ± 4 |
| 121-130 | >40 | 10 | 120 ± 5 |
| | Managed Forests | | |
| 51-60 | 475 | 10 | 55 ± 2 |
| 71-80 | 1,688 | 8 | 66 ± 5 |
| 91-100 | 510 | 10 | 72 ± 5 |
| 111-120 | 43 | 10 | 91 ± 7 |

[1]n = 24 for age. [2]n = 19 for age.

100 $m^2$ plot. Values for all variables measured on the 2, 20, and 100 $m^2$ plots were averaged to yield a single value for the entire sample plot.

### Vegetation Measurements

Overstory age for each plot was determined by coring the nearest dominant or co-dominant tree to the plot center. We cored the tree at dbh (diameter at breast height; 1.37 m above ground) using an increment borer. Age at dbh was estimated by counting tree rings.

For all overstory trees with dbh ≥ 15 cm in each 1000 $m^2$ plot, we recorded species, dbh, and crown ratio (visual estimate of live crown as percent of total height). Total height was measured directly with a Spiegel Relaskop on 50-75% of the trees per plot. The heights of the rest of the trees were then estimated by visual reference to the trees with known heights. Crown depth was calculated as (live crown ratio x tree height / 100). Trees forked below dbh were measured as two individual trees.

Percent cover was estimated visually for the overstory and shrub (maximum plant height ≥ 0.2 m) layers on the 1000 $m^2$ and 500$m^2$ plots, and for the ground layer (maximum plant height < 0.2 m) on each 20 $m^2$ plot. Plant nomenclature follows Hitchcock and Cronquist (1973).

Presence of all shrub and ground-layer species was recorded in each 20 $m^2$ plot, except for grasslands (age zero). We used these data to estimate shrub and ground-layer species richness. For grasslands, we calculated species richness from ground-layer species tallies made in the same year as our study along 100-m-long line transects (n = 84) randomly placed in five different Fort Lewis grasslands (Angela Lombardi, Fort Lewis Integrated Training Area Management Program, personal communication). We assumed that the species composition along these transects was similar to that in the 10 plots established in our study.

### Dead Wood Measurements

Within each 1000 $m^2$ plot, we tallied all snags with dbh ≥ 15 cm and height ≥ 1 m, and measured the length of all logs with a small-end diameter ≥ 10 cm and length ≥ 1 m. Branches < 5 cm diameter at the small end, plus twigs, needles, and cones (collectively referred to as litter) on the surface of the forest floor were collected from each 2 $m^2$ plot, oven-dried at 30°C for ≥ 5 d, and weighed. Litter biomass (g/$m^2$) was calculated by dividing litter dry mass by the area of the plot.

### Soil Measurements

We placed a 1 x 1 m frame at each 1000 $m^2$ plot center and secured it with metal stakes. The O horizon (forest floor) within the frame was removed and weighed in the field. The sample was mixed and a 20-g subsample weighed, oven-dried at 30° C for ≥ 5 d, and reweighed. We calculated biomass (g/$m^2$) of the O horizon as (total sample fresh weight x [subsample dry weight / subsample fresh weight]).

The A horizon was sampled by excavating a hole with dimensions 30 x 30 x 25 cm depth, centered within the frame. The soil was sieved to remove the coarse fraction (≥ 2 mm), weighed, and a 200-g subsample of the fine fraction (< 2mm) was oven-dried at 30° C for ≥ 5 d.

We placed the dried subsamples of the O and A horizons in ziploc bags and sent them to the Analytical Sciences Laboratory at the University of Idaho. There, total nitrogen of the O horizon and total nitrogen and carbon of the A horizon were measured with a Leco high-temperature combustion analyzer; the results are expressed as percent dry mass of the fine fraction. A-horizon pH was measured in a saturated paste and A-horizon cation-exchange capacity (CEC) was determined with the ammonium acetate test (Page et al. 1982).

### Statistical Analysis

We analyzed the data with one-way analysis of variance (ANOVA), separately for managed and unmanaged forests, to ascertain differences between age-class means for each variable. The level of significance was 0.05. If an ANOVA was significant, we compared age-class means with the Bonferonni procedure (Day and Quinn 1989). We also compared means of managed and unmanaged forests of similar age using *t*-tests, with a significance level of 0.05. Prior to statistical analysis, we transformed data sets that did not meet the assumptions of normality and homoscedasticity. All analyses utilized SigmaStat 2.0 software (Fox et al. 1995).

## Results

### Plot Ages

Mean plot ages within each forest age class were highly variable and did not always correspond closely to ages indicated on the GIS age-class map (Table 1). Three pairs of unmanaged/managed age

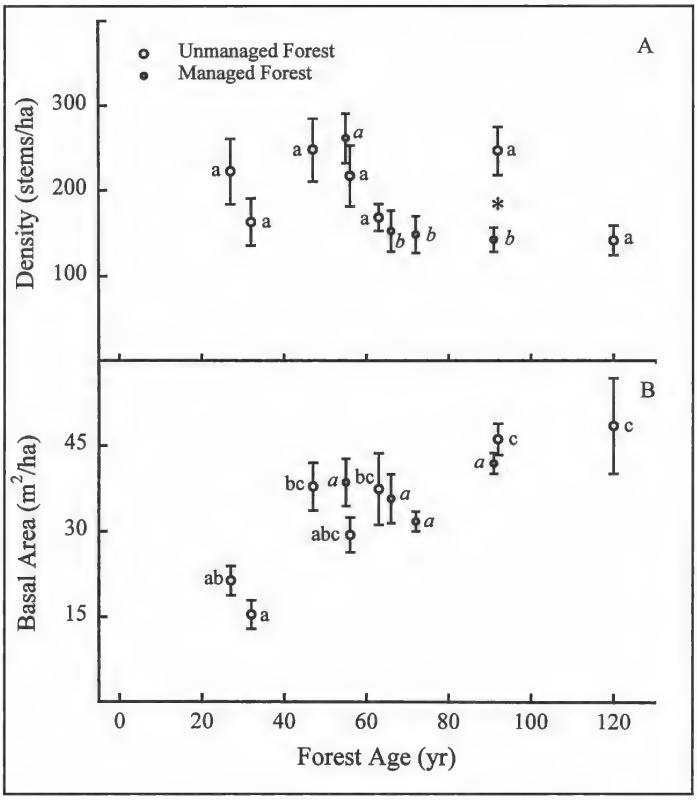


Figure 1. Overstory tree density (A) and basal area (B) in unmanaged and managed forests. Data are means (± 1 SE). Within unmanaged and managed forests, means with the same lowercase letter (normal font for unmanaged forests, italic font for managed forests) are not significantly different. Asterisks indicate when the means of unmanaged and managed forests of similar age are significantly different.

classes (56 vs. 55, 63 vs. 66, and 92 vs. 91 yr) had mean plot ages that did not differ significantly; these were used for comparing unmanaged and managed forests of similar ages.

## Vegetation

Virtually all overstory trees were Douglas-fir. Overstory tree density showed no trend over time in unmanaged forests (Figure 1A). In contrast, tree density decreased by 40 stems/ha between 56 and 63 yr in managed forests ($P < 0.01$), and was lower at 92 yr in managed than in unmanaged forests of similar age ($P < 0.01$) (Figure 1A). Overstory basal area increased over time in umanaged forests ($P < 0.001$), more than doubling between 27-32 yr and 120 yr. There was no trend in basal area of managed forests, and it did not differ significantly from that of unmanaged forests at any age (Figure 1B). Mean crown depth did not change significantly with age in unmanaged or managed forests, but was 25% lower in 91-yr-old unmanaged forests than in managed forests of similar age ($P < 0.01$) (Table 2).

Overstory cover in unmanaged forests increased gradually between 27-32 yr and 92 yr ($P < 0.001$) (Figure 2A). In managed forests, overstory cover remained constant over time, and was lower than in umanaged forests at 91 yr ($P < 0.001$) (Figure 2A). Shrub cover in unmanaged forests increased steadily from 3% in grasslands to 45% at 120 yr ($P < 0.001$) (Figure 2B). In contrast, there was no trend in shrub cover in managed forests,

TABLE 2. Mean (± 1 SE) of several vegetation, dead wood, and soil attributes in unmanaged and managed forests. Within columns, means with the same letter superscript are not significantly different. Asterisks indicate significantly different means for unmanaged and managed forests of similar age. Age 0 yr represents grassland plots.

| Forest Age (yr) | Crown Depth (m) | Biomass Litter ($g/m^2$) | Biomass O-Horizon ($kg/m^2$) | A-Horizon pH (units) | O-Horizon Nitrogen (%) |
|---|---|---|---|---|---|
| | | Unmanaged Forests | | | |
| 0 | n/a | $1 \pm 0^{a}$ | $1.05 \pm 0.12^{a}$ | $5.44 \pm 0.04^{a}$ | $1.19 \pm 0.05^{a}$ |
| 27 | $11.5 \pm 0.8^{a}$ | $21 \pm 5^{abc}$ | $1.03 \pm 0.27^{a}$ | $5.40 \pm 0.04^{a}$ | $1.15 \pm 0.05^{a}$ |
| 32 | $12.9 \pm 0.8^{a}$ | $28 \pm 14^{bc}$ | $1.11 \pm 0.13^{a}$ | $5.22 \pm 0.04^{ab}$ | $1.33 \pm 0.06^{a}$ |
| 47 | $12.2 \pm 0.7^{a}$ | $33 \pm 8^{bc}$ | $1.09 \pm 0.14^{a}$ | $5.33 \pm 0.03^{ab}$ | $1.18 \pm 0.06^{a}$ |
| 56 | $14.8 \pm 2.8^{a}$ | $33 \pm 8^{bc}$ | $0.59 \pm 0.07^{a}$ | $5.26 \pm 0.05^{ab}$ | $1.32 \pm 0.07^{a}$ |
| 63 | $13.7 \pm 1.2^{a}$ | $20 \pm 5^{ab}$ | $1.07 \pm 0.20^{a}$ | $5.18 \pm 0.06^{b*}$ | $1.39 \pm 0.05^{a*}$ |
| 92 | $10.5 \pm 0.6^{a*}$ | $49 \pm 13^{bc}$ | $0.87 \pm 0.29^{a}$ | $5.34 \pm 0.09^{ab}$ | $1.27 \pm 0.07^{a}$ |
| 120 | $13.7 \pm 1.5^{a}$ | $37 \pm 8^{bc}$ | $0.89 \pm 0.21^{a}$ | $0.29 \pm 0.08^{ab}$ | $1.06 \pm 0.15^{a}$ |
| | | Managed Forests | | | |
| 55 | $12.7 \pm 1.4^{a}$ | $31 \pm 5^{a}$ | $1.02 \pm 0.23^{a}$ | $5.24 \pm 0.09^{a}$ | $1.23 \pm 0.16^{a}$ |
| 66 | $15.2 \pm 1.7^{a}$ | $36 \pm 8^{a}$ | $0.99 \pm 0.10^{a}$ | $5.34 \pm 0.03^{a*}$ | $1.17 \pm 0.09^{a*}$ |
| 72 | $14.6 \pm 0.8^{a}$ | $40 \pm 12^{a}$ | $0.69 \pm 0.11^{a}$ | $5.29 \pm 0.06^{a}$ | $1.54 \pm 0.09^{a}$ |
| 91 | $14.4 \pm 1.0^{a*}$ | $25 \pm 5^{a}$ | $0.69 \pm 0.11^{a}$ | $5.37 \pm 0.10^{a}$ | $1.39 \pm 0.04^{a}$ |

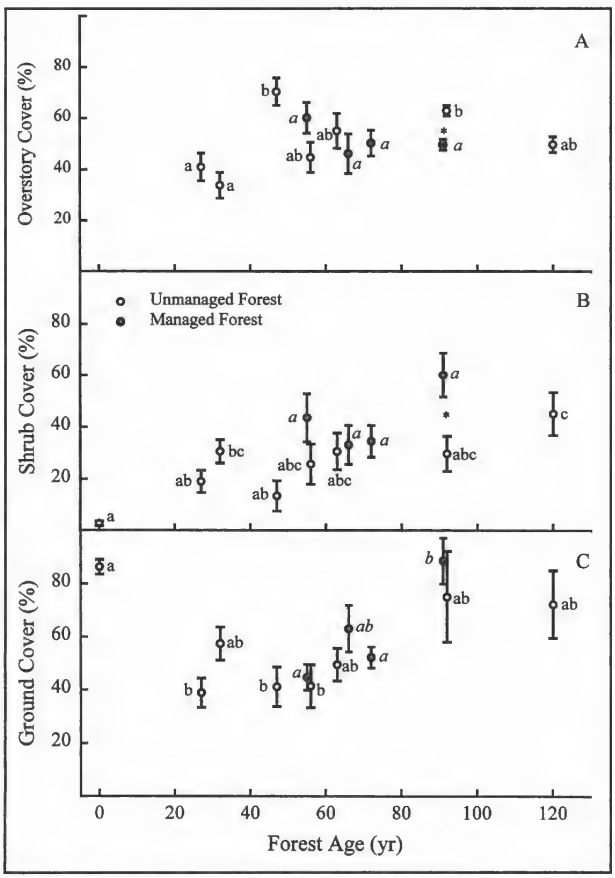


Figure 2. Overstory (A), shrub (B), and ground-layer (C) cover in unmanaged and managed forests. Data are presented in the same manner as Figure 1.

although it was twice as high at 91 yr as in unmanaged forests of similar age ($P < 0.05$) (Figure 2B). Ground cover was generally less in unmanaged forests ≤ 56-yr-old than in grasslands, but was similar to grasslands in older unmanaged forests ($P < 0.001$) (Figure 2C). In managed forests, ground cover increased between 72 and 91 yr ($P < 0.001$), but did not differ significantly from that of unmanaged forests at any age (Figure 2C).

Species richness in the ground layer was 75% less, but shrub species richness was the same, in 27-yr-old unmanaged forests compared to grasslands ($P < 0.001$) (Figure 3); thereafter, both ground-layer and shrub species richness increased gradually (to 63 yr in unmanaged forests, 72 yr in managed forests) ($P < 0.001$), then remained constant (Figure 3). With increasing age in managed forests, ground-layer species richness increased ($P < 0.01$), but shrub species richness remained constant, and neither differed between unmanaged and managed forests of similar age (Figure 3). A total of 136 species occurred in grasslands. Eight of these species were present in the oldest (120 yr) unmanaged forests and seven in the oldest (91 yr) managed forests.

## Dead Wood

Snag density in 27- to 32-yr-old unmanaged forests was 7-8 stems/ha, then increased 10-fold by 92 yr ($P < 0.001$) (Figure 4A). In contrast, there was no trend in snag density in managed forests, and it did not differ significantly between unmanaged and managed forests of similar age (Figure 4A). Total log length in unmanaged forests increased over time ($P < 0.001$), from near zero at 27-32 yr to 140 m/ha at 120 yr (Figure 4B). Log length did not change over time in managed forests, and by 92 yr it was lower than in unmanaged forests of similar age ($P < 0.05$) (Figure 4B). Litter biomass in unmanaged forests increased

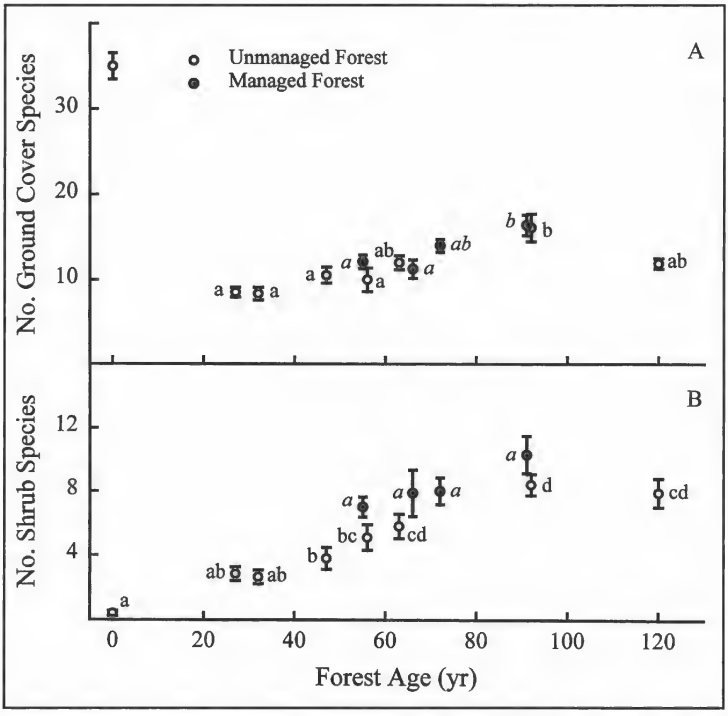


Figure 3. Species richness of ground (A) and shrub (B) layers in unmanaged and managed forests. Data are presented in the same manner as Figure 1. Ground-layer diversity at age 0 yr (grassland) was measured by a different method than the rest of the data, and was excluded from the statistical analysis.

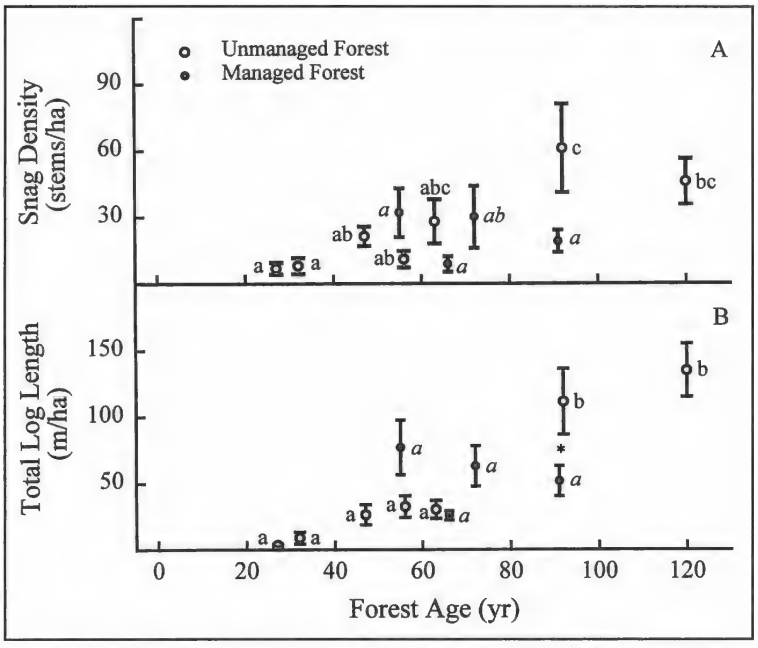


Figure 4. Snag density (A), total log length (B), and forest floor litter (C) in unmanaged and managed forests. Data are presented in the same manner as Figure 1.

from near zero in grasslands to 28 g/m$^2$ at 32 yr ($P < 0.001$), and remained constant thereafter; in managed forests, it remained constant over time (Table 2).

### Soils

O-horizon biomass showed no temporal trends in either unmanaged or managed forests, and did not differ significantly between unmanaged and managed forests of similar age (Table 2). A-horizon pH did not change over time in either unmanaged or managed forests, and was slightly lower (0.16 units) in 63-yr-old unmanaged forests than in managed forests of similar age ($P < 0.05$) (Table 2). In unmanaged forests, A-horizon CEC varied over time ($P < 0.001$), with a minimum at 27 yr and a maximum at 56-92 yr (Figure 5A). In managed forests, CEC increased nearly two-fold between 55 and 91 yr ($P < 0.001$), from being less than to more than unmanaged forests of similar age ($P < 0.05$) (Figure 5A).

The carbon concentration of the A-horizon in unmanaged forests did not change over time, while that of managed forests increased 50% between 55 and 91 yr ($P < 0.05$), going from lower than to higher than unmanaged forests of similar age ($P < 0.05$) (Figure 5B). O-horizon nitrogen concentration did not change over time in either unmanaged or managed forests, but was lower in 66-yr-old managed forests than in unmanaged forests of similar age ($P < 0.05$) (Table 2). A-horizon nitrogen in unmanaged forests declined about 40% between 56 and 120 yr ($P < 0.001$), while in managed forests it more than doubled over time ($P < 0.05$), from being less than to more than unmanaged forests of similar age ($P < 0.01$) (Figure 5C).

## Discussion

### Ecosystem Changes in Unmanaged Forests

The major consequence of fire exclusion in southern Puget Lowland grasslands is rapid (< 30 yr) conversion to forest, with a shift from complete dominance by grasses and forbs to complete dominance by woody species, accompanied by a major floristic turnover from grassland- to forest-associated

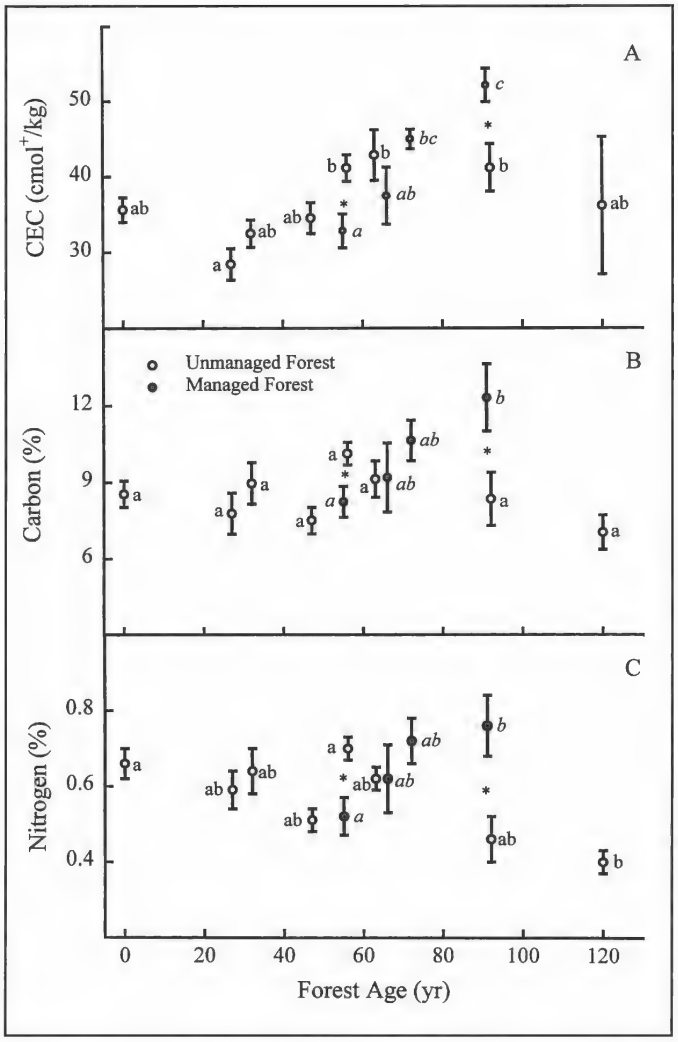


Figure 5. A-horizon cation-exchange capacity (A), and carbon (B) and nitrogen (C) concentrations, in unmanaged and managed forests. Data are presented in the same manner as Figure 1.

species. In the absence of fire, tree or shrub invasion of mesic grasslands in other parts of the world can occur with similar rapidity (Knight et al. 1994, Bruce et al. 1995, Arabas 2000, Briggs et al. 2002). A drastic reduction in herbaceous species richness is also typical of grassland invasions (Archer 1995, Bruce et al. 1995, Briggs et al. 2002, Miller and Tausch 2001).

The wide range of overstory tree ages for the seven age classes of unmanaged forests, $41 \pm 5$ yr, implies that the trees in Fort Lewis' colonization forests became established over periods of decades, as would be expected if tree invasion was patchy. Peterson and Hammer (2001) also found a wide range (50-95 yr) in overstory Douglas-fir tree ages in a colonization forest on Orcas Island, Washington.

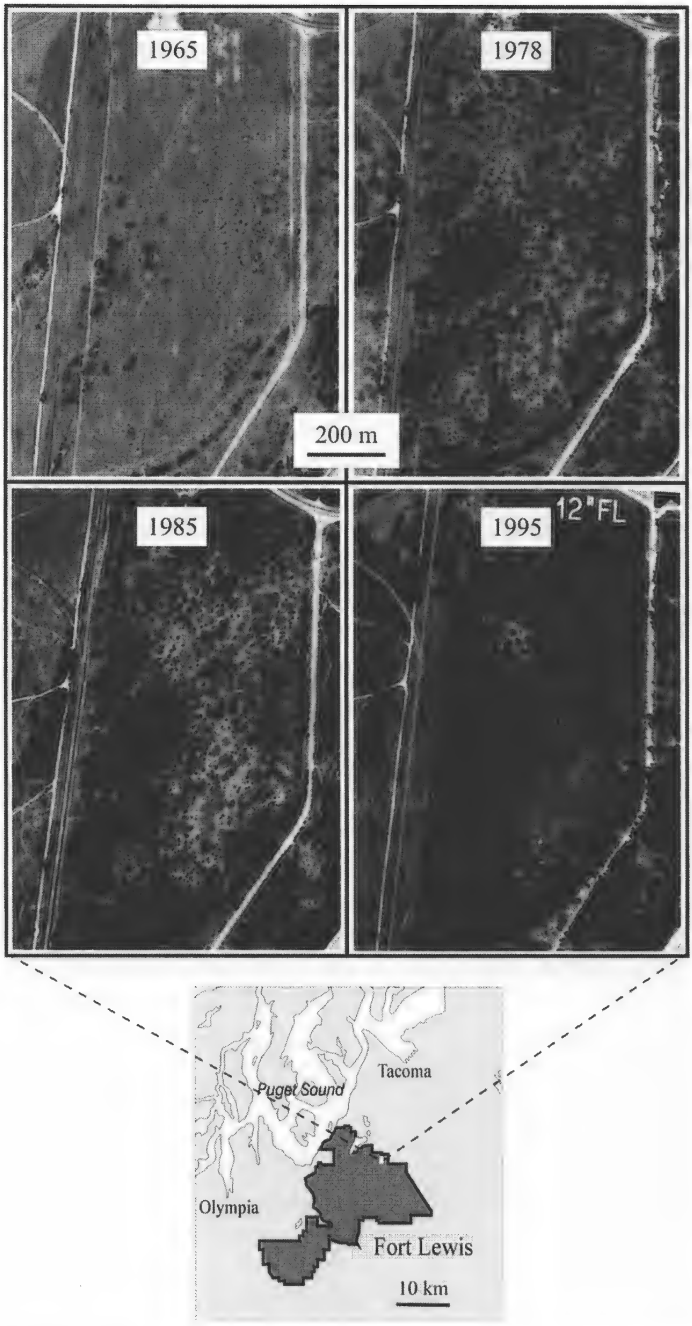


Figure 6. Time series of aerial photographs of a portion of Fort Lewis that has been undergoing Douglas-fir tree invasion.

At Fort Lewis, direct confirmation of the patchy nature of tree invasion is provided by time series of aerial photographs, which reveal that young, unmanaged colonization forests consist of small groves of dense young conifers separated by areas of few or no trees. These groves later merge as newly established trees fill in the remaining openings between the patches (Figure 6). This is the same process observed by Giles (1970) on Mima Prairie, west of Fort Lewis. In southern Texas grasslands, initial invasion by mesquite (*Prosopis glandulosa*) takes the form of scattered shrub clusters. Expansion and coalescence of existing clusters and initiation of new clusters eventually results in conversion to mesquite woodland (Archer et al. 1988). A patchy pattern was also inferred for Virginia pine (*Pinus virginiana*) invasion of serpentine barrens in Pennsylvania (Barton and Wallenstein 1997).

At Fort Lewis, maximum canopy cover of 45-65%, attained by 42 yr, allows sufficient light to reach the forest floor for ground cover to persist and for the gradual development of a shrub layer. In contrast, succession after fire or logging on moister sites in western Washington and Oregon typically passes through a stem-exclusion phase characterized by a dense conifer overstory and almost total absence of ground and shrub cover (Oliver and Larson 1996). Woody plant invasion of grasslands elsewhere in North America results in a decline in herbaceous cover and productivity, initially underneath individual trees or shrubs, and later for the plant community as a whole, while shrub growth is either inhibited or facilitated by the invading species (Archer 1995, Bruce et al. 1995, Briggs et al. 2002, Miller and Tausch 2001).

Another important change in ecosystem structure associated with tree invasion at Fort Lewis is the accumulation of dead wood. However, the absolute amounts, especially of large snags and logs, are much less than in mature conifer forests elsewhere west of the Cascade Mountains. For example, in the oldest (120-yr-old) colonization forests, snag density (≥ 10 cm dbh) was 46 stems/ha and log density (≥ 10 cm diameter) was 222 pieces/ha, compared to 121 stems/ha and 447 pieces/ha for the same size classes of snags and logs in 80- to 199-yr-old Douglas-fir forests in western Oregon (Spies et al. 1988).

The primary effect of tree invasion on Fort Lewis soils is a substantial decrease in A-horizon nitrogen. This is likely a consequence of the accumulation and decay of woody litter with a higher C:N ratio than the almost exclusively herbaceous litter of grasslands. Unlike nitrogen, soil carbon does not accumulate, nor are there long-term trends in soil pH or CEC. Everett soils, which occur on dry sites that have been forested for centuries, and which may represent the end-point of forest invasion of Puget Lowland grasslands, have A-horizon nitrogen concentrations that are half those of Spanaway soils, but the two soil types do not differ in pH (Ugolini and Schlichte 1973). Previous studies have found that soil nitrogen increases when junipers (*Juniperus* spp.) invade Great Basin shrub-steppe (Miller and Wigand 1994) and when creosote bush (*Larrea tridentata*) invades New Mexico grasslands (Gill and Burke 1999), and that both soil carbon and soil nitrogen increase when mesquite invades Texas grasslands (Archer 1995). These studies examined soils beneath individual trees or shrub clumps, and thus are not directly comparable to our study. Barton and Wallenstein (1997), however, observed that when Virginia pine invades serpentine barrens, soil organic matter increases beneath individual trees, but there is no difference in soil organic matter between entire stands of pine savanna (earlier stage of succession) and closed pine forest (later stage of succession).

How long might it take for grassland soils to be transformed into forest soils as a result of tree invasion? The answer is certainly centuries, since even the oldest colonization stand on Fort Lewis, 400-yr-old Ellsworth Woods, is partially underlain by grassland soils (Glenn Ahrens, GBA Forestry, Astoria, Oregon, personal communication). In southern Minnesota, fossil pollen reconstruction of Holocene vegetation, when compared to the modern distribution of soils, suggests that it requires several thousand years of oak woodland invasion of grasslands for grassland soils to become woodland soils, and that 300 yr of invasion of woodlands by deciduous forest have not yet converted woodland soils to forest soils (Grimm 1983).

Colonization forests are scattered across Pierce, Thurston, Lewis, Mason, and eastern Grays Harbor counties in the southern Puget Lowland. These are underlain by the same (Spanaway, Fitch, Nisqually) or similar (Carstairs) grassland soil series as Fort Lewis (Crawford and Hall 1997).

Due to the similarities in soils, topography, and climate, we believe the successional trends in unmanaged colonization forests observed at Fort Lewis are typical of trends in unmanaged colonization forests across the region.

## Influences of Timber Harvest

The typical stand age at first thinning on Fort Lewis is 50-60 yr and thinnings are relatively light (average removal of stems ≥ 20 cm dbh in 79 thinning sales between 1997 and 2001 was 16%), thus it is not surprising that differences in vegetation structure between unmanaged and managed forests are few (lower canopy cover, higher shrub cover) and do not appear until 91 yr of age. Timber harvest also has no effect on the species richness of the shrub and ground layers, or on the persistence of grassland species in older colonization forests.

The lack of accumulation of snags and logs in managed forests can be attributed to the pre-1991 Fort Lewis policy to remove sound snags and logs during timber harvest. Under current policy, sound snags and logs remain in the woods and most senescent trees, which will eventually become snags, also remain. Therefore, we expect dead wood accumulation in the future in managed forests.

We attribute the positive effect of timber harvest on CEC, nitrogen, and carbon in the A horizon to mixing of the litter layer and the O horizon with the A horizon by heavy logging equipment during timber harvests. The resulting increased organic matter content of the A horizon causes A-horizon CEC, carbon, and nitrogen to increase. Mixing also explains why managed and unmanaged forests have similar amounts of litter, despite the presence of logging-generated slash in managed forests.

Management of southern Puget Lowland colonization forests outside Fort Lewis is usually quite different from that on the installation. Clearcut and shelterwood timber harvests are common, some forests are grazed or managed for firewood, and none has military activity. Therefore, the influences of timber harvest observed in this study may be unique to Fort Lewis.

## Management Implications

Most colonization forests on Fort Lewis are < 100 yr old, thus lack large live trees, one component of spotted owl habitat. Colonization forests also have little large dead wood, e.g., of the snags (≥ 60 cm dbh and 6 m tall) and logs (≥ 50 cm diameter and 6 m long) that are another component of owl habitat (USDA Forest Service & USDI Bureau of Land Management 1994), only one snag and 30 logs occurred across all the plots in this study. In addition, colonization forests have little shade-tolerant western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*), species that contribute to the development of multiple canopy layers, a third component of owl habitat. Therefore, colonization forests are not currently owl habitat, and will not become owl habitat for more than a century. However, continued periodic thinnings, by increasing the growth rates of residual trees, will hasten the appearance of large live trees. Deliberate snag and log creation and underplanting of shade-tolerant species could further accelerate development of owl habitat.

Forest invasion has decreased the likelihood of wildfires at Fort Lewis. The majority of ignitions occur during summer droughts, when fuel moisture is low, and in grasslands, where tracer bullets, pyrotechnics, and artillery shells are used (Joe Reasoner, Fort Lewis Forestry Program, personal communication). Because forest understory fuels take longer to dry out after rain than do grassland fuels, ignitions are less likely in forests than in grasslands. Installation records indicate that between 1986 and 2000, a much greater area of grassland than of forest or woodland burned in wildfires, even though Fort Lewis has more than twice the area of forests and woodlands as it has grasslands. However, during extended droughts, the potential for crown fires is substantial in colonization forests because of large fuel loads, especially midstory fuels (e.g., shrubs) that can carry fire from the ground into the overstory. The difference in wildfire risk during drought between forests and grasslands is probably greater today than prior to settlement because colonization forests have substantially higher tree densities than did the original forests of Fort Lewis, as indicated by land-survey records from the mid-19th century (Public Forestry Foundation 1996). Peterson and Hammer (2001) reached the same conclusion for the colonization forest on Orcas Island, Washington. Miller and Tausch (2001) found that when semiarid grasslands are invaded by junipers, the decrease in understory biomass beneath individual junipers initially reduces wildfire risk, but later, as juniper woodlands with closed canopies develop, the risk of crown fire increases substan-

tially. In southern Minnesota, grassland conversion to oak woodland substantially decreased fire frequency (Grimm 1983).

Will the trend of decreasing soil nitrogen in unmanaged forests eventually reduce tree growth? There is a twofold difference in soil nitrogen between Spanaway and Everett soils (Ugolini and Schlichte 1973), the latter being the putative endpoint of soil development when trees invade Puget Lowland prairies. However, stand inventory data (Lathrop Leonard, Fort Lewis Forestry Program, personal communication) indicate that almost all Fort Lewis forests, on both Spanaway and Everett soils, are Douglas-fir site-index class II (King 1966), suggesting that the reduced soil nitrogen does not influence site productivity. Conversely, if soil nitrogen continues to increase in managed forests, will tree growth eventually increase? This is difficult to answer because in managed forests, the potential growth effects of higher nitrogen are confounded with those of thinning. Factorial thinning and fertilization trials in unmanaged forests are required to separate these two potential effects.

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## Literature Cited

Ahrens, G. R. 1998a. Ecology of dry Douglas-fir forests: focus on Fort Lewis, Washington. Unpublished report by The Nature Conservancy, on file at the Forestry Program, Fort Lewis, Washington.

Ahrens, G. R. 1998b. Tree mortality and coarse woody debris in the Fort Lewis forest. Unpublished report by The Nature Conservancy, on file at the Forestry Program, Fort Lewis, Washington.

Anderson, W. W., A. O. Ness, and A. C. Anderson. 1955. Soil survey of Pierce County, Washington. USDA Soil Conservation Service, Washington, D.C.

Arabas, K.B. 2000. Spatial and temporal relationships among fire frequency, vegetation, and soil depth in an eastern North American serpentine barren. Journal of the Torrey Botanical Society 127:51-65.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. EcoScience 2:83-99.

Archer, S. 2003. Woody plant encroachment bibliography. Department of Rangeland Ecology & Mangement, Texas A&M University, College Station, Texas. Available online at cnrit.tamu.edu/rlem/faculty/archer/bibliography.html/.

Archer, S., C. Scifres, and C. R. Bassham. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:111-127.

Bailey, A. W., and R. A. Wroe. 1974. Aspen invasion in a portion of the Alberta parklands. Journal of Range Management 27:263-266.

Barton, A. M., and M. D. Wallenstein. 1997. Effects of invasion of *Pinus virginiana* on soil properties in serpetine barrens in southeastern Pennsylvania. Journal of the Torrey Botanical Society 124:297-305.

Briggs, M. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578-586.

Bruce, K. A., G. N. Cameron, and P. Harcombe. 1995. Initiation of a new woodland type on the Texas coastal prairie by the Chinese tallow tree (*Sapium sebiferum*). Bulletin of the Torrey Botanical Club 122:215-225.

Crawford, R. C., and H. Hall. 1997. Changes in the South Puget Sound grassland landscape. Pages 11-15 *In* P. V. Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Grassland Landscape. The Nature Conservancy, Seattle, Washington.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433-463.

Fox, E., K. Shotton, and C. Ulrich. 1995. SigmaStat Statistical Software User's Manual. Jandel Corporation, San Rafael, California.

Giles, L. J. 1970. The ecology of the mounds on Mima Prairie with special reference to Douglas-fir invasion. M.S. Thesis, University of Washington, Seattle, Washington.

Gill, R. A., and I. C. Burke. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. Oecologia 121:551-563.

Grimm, E. C. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, U.S.A. New Phytologist 93:311-350.

Hibbert, D. M. 1979. Pollen analysis of late-Quaternary sediments from two lakes in the southern Puget Lowlands, Washington. M.S. Thesis, University of Washington, Seattle, Washington.

Hitchcock, C.L. and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington.

King, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser Forestry Paper No. 8. Weyerhaeuser Company, Centralia, Washington.

Knight, C. L., J. M. Briggs, and M. D. Nellis. 1994. Expansion of gallery forest on Konza Prairie Prairie Research Natural Area, Kansas, USA. Landscape Ecology 9:117-125.

Kruckeberg, A. R. 1991. The Natural History of Puget Sound Country. University of Washington Press, Seattle, Washington.

Miller, R. F., and R. J. Tausch. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. Pages 15-30 *In* K. E. M. Galley and T. P. Wilson (editors), Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Miscellaneous Publication No. 11. Tall Timbers Research Station, Tallahassee, Florida.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semiarid pinyon-juniper woodlands. BioScience 44:465-474.

Oliver, C. D., and B. C. Larson. 1996. Forest Stand Dynamics. Wiley, New York.

Page, A. L., R. H. Miller, and D. R. Keeney, editors. 1982. Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. American Society of Agronomy/Soil Science Society of America, Madison, Wisconsin.

Perdue, V. 1997. Land use and the Fort Lewis grasslands. Pages 17-28 *In* P. V. Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Grassland Landscape. The Nature Conservancy, Seattle, Washington.

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Peterson, D. L., and R. D. Hammer. 2001. From open to closed canopy: a century of change in a Douglas-fir forest, Orcas Island, Washington. Northwest Science 75:262-269.

Pringle, R. F. 1990. Soil survey of Thurston County, Washington. USDA Soil Conservation Service, Washington, D.C.

Public Forestry Foundation. 1996. A forest management strategy for the Fort Lewis Military Reservation, Fort Lewis, Washington. Unpublished report on file with the Forestry Program, Fort Lewis, Washington.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1689-1702.

Ugolini, F. C., and A. K. Schlichte. 1973. The effects of Holocene environmental changes on selected western Washington soils. Soil Science 116:218-227.

U.S. Army Corps of Engineers. 1994. Final environmental impact statement: stationing of mechanized or armored combat forces at Fort Lewis, Washington. Mobile, Alabama.

USDA Forest Service & USDI Bureau of Land Management. 1994. Standards and guidelines for management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. Washington, D.C.

Whitlock, C. 1992. Vegetational and climatic history of the Pacific Northwest during the last 20,000 years: implications for understanding present-day biodiversity. Northwest Environmental Journal 8:5-28.

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# Carbon Storage and Soil Properties in Late-successional and Second-growth Subalpine Forests in the North Cascade Range, Washington

## Abstract

We compared soil carbon (C) and soil chemical characteristics between late-successional subalpine forests and adjacent regenerating clearcuts (20-40 yr post harvest) that received different logging residue treatments (burned vs. unburned) at four sites in the North Cascade Range of Washington. Carbon storage in the O horizon and mineral soil, C concentration, and soil chemical properties in the mineral soil and spodic horizons were compared between forests and clearcuts, and between burned and unburned clearcuts. Mean carbon storage was 131.3 Mg $ha^{-1}$ in clearcuts and 95.4 Mg $ha^{-1}$ in forests. Mean C concentration was 55.3 g $kg^{-1}$ in unburned clearcuts and 45.1 g $kg^{-1}$ in burned clearcuts. Several soil chemical properties were correlated with C concentrations, although causation of patterns was difficult to infer. Calcium (Ca) concentration was significantly higher in mineral soils of clearcuts than in uncut forests, with unburned clearcuts having the highest Ca concentration. This is a potentially important change in chemical cycling, because subalpine soils have low cation content. Clearcut logging may affect post-harvest soil C storage and other soil properties on a temporary basis, but with the exception of Ca, no long-term effects were apparent at these sites. Post-harvest burning appeared to have a minimal effect 20-40 yr following logging.

## Introduction

Soils underlying subalpine forests are important reservoirs of carbon (C) in the Pacific Northwest region of North America (Grier et al. 1981, Johnson et al. 1982, Prichard et al. 2000). Low temperatures slow the microbial breakdown of organic matter resulting in long residence times and relatively large quantities of belowground C, especially in Spodosols (Edmonds 1980, Powers and Van Cleve 1991, Kirschbaum 1995). Additionally, a consistent supply of soil water, from rainfall and snowmelt, may leach C into deeper horizons where it persists in more stable forms and is less subject to mineralization (Kuramoto and Bliss 1970, Vogt et al. 1989, Stone et al. 1993, Richter et al. 1995, Christensen et al. 1999).

Forest harvest can alter site conditions that influence decomposition rates and C stabilization mechanisms so that soils are converted from sinks to sources of atmospheric C (Powers 1980, Johnson et al. 1995, Rustad and Fernandez 1998, MacDonald et al. 1999). Even if total soil C quantities are not affected by tree harvest, redistribution of C within the soil profile is likely because of leaching and mechanical disturbance by logging equipment (Johnson et al. 1991, Ryan et al. 1992). Because soil organic matter provides most of the cation exchange capacity (CEC) of Spodosols (Federer and Hornbeck 1985), essential nutrients may be transported along with C deeper into the soil profile. Nutrients then may be initially less available for regrowing plants (Snyder and Harter 1984, Johnson et al. 1995, Johnson et al. 1997), thereby affecting forest productivity.

Little information exists on the effects of timber harvest on soil C in subalpine forest systems. The effects of harvest activities on temperate and tropical forest soils are extremely varied (Johnson 1992, Johnson and Curtis 2001). Most effects on soil C storage and distribution appear to be associated with one or more variables related to specific characteristics of (1) site (e.g., dominant vegetation, soils, climate) (Borchers and Perry 1992, Knoepp and Swank 1997), (2) harvest practices (Kraemer and Hermann 1979, Edwards and Ross-Todd 1983, Burger and Pritchett 1984, Miller and Sirois 1986, Mattson and Swank 1989, Johnson and Todd 1998, Piatek and Allen 1999, Bock and Van Rees 2002), and (3) study design (e.g., time since harvest, sampling depth) (Covington 1981, Black and Harden 1995, Johnson et al. 1995,

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Knoepp and Swank 1997). Generally, there is a post-harvest pulse of C and nutrients to the soil. This pulse may be immediate when residues are burned (Adams and Boyle 1980), or occur more slowly when on-site residues are allowed to decompose (Entry and Emmingham 1998). The longevity of the period of higher C depends on environmental conditions that control decomposition, however, soil C content generally decreases over time after timber harvest (Alban and Perala 1992, Johnson 1992, Knoepp and Swank 1997, Johnson and Todd 1998).

Because decomposition rates are exceptionally slow in subalpine forest systems, the presence or absence of logging residues may affect soil C and chemical characteristics over a longer temporal scale than in low-elevation forests. In this study, we quantified soil C and other physical and chemical characteristics of the soil profile in late-successional subalpine forests and adjacent stands clearcut 20-40 yr ago in the North Cascade Range, Washington. Clearcut sites with and without post-harvest burning treatments were included in the analysis to evaluate the combined effects of logging and slash burning on subalpine soils.

## Methods

### Study Area

The study is in subalpine forests in a portion of the Mt. Baker-Snoqualmie National Forest that is northwest of Mt. Baker, the northernmost of the Cascade Range volcanoes (Figure 1). This portion of the North Cascades is steep, rugged, and composed of sedimentary and metamorphic formations that have been glacially modified. The resulting landscape is a mosaic of broad valleys, cirques, arêtes, and morainal and outwash deposits that is heavily dissected by many streams.

The North Cascades create an orographic barrier to weather systems moving inland from the Pacific Ocean, resulting in cool, wet winters (with high snowfall at higher elevations) and mild summers characterized by a period of low precipitation on the western slopes. Mean annual temperature is 5° C within the study area; January and July means are –2° and 14° C. Mean winter precipitation (November–February) at Wells Creek, the nearest Snotel weather station (elevation 1561 m) is 278 cm, the majority falling as snow and

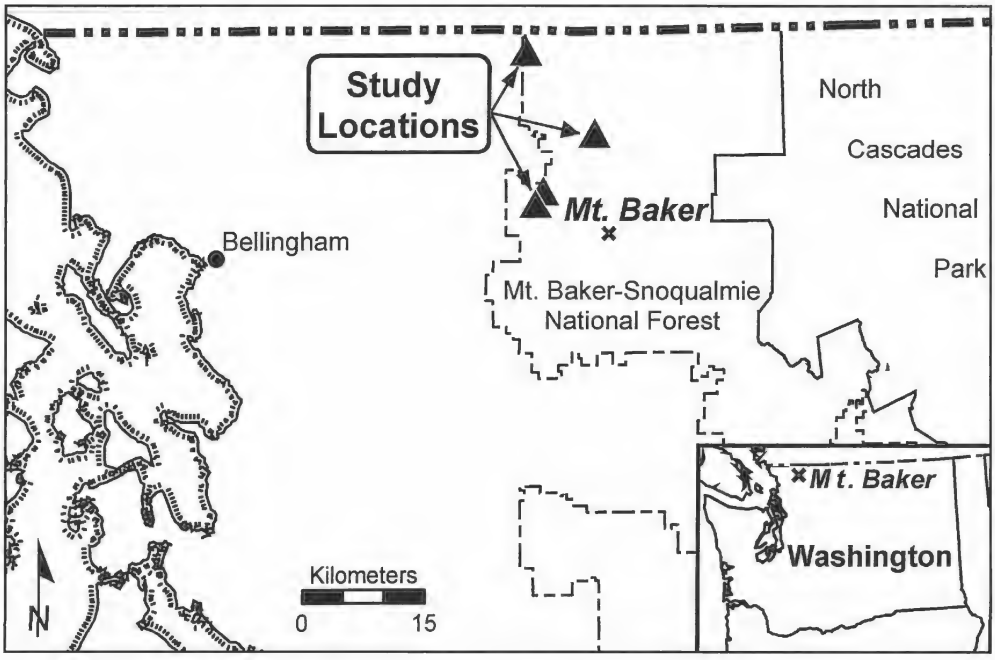


Figure 1. Location of the four study sites in the North Cascade Range.

accumulating in deep, persistent snowpacks. Mean summer precipitation (June–September) is 89 cm.

Spodosols, often skeletal, are common in the high-elevation forests of the study area. Soils have developed in hillslope sediments and tephra over sedimentary rock. Curved tree trunks and absence of A horizons are manifestations of soil creep on the steep slopes of the study area. Buried horizons in forests and clearcuts are evidence of mass wasting events. Soils are well-drained Typic Haplocryods and Typic Humicryods (Soil Survey Staff 1999).

Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) dominate forest overstories, while moss, woody debris, rustyleaf (*Menziesia ferruginea*), Alaska huckleberry (*Vaccinium alaskaense*), and Pacific silver fir seedlings are common in the understories. Subalpine fir (*Abies lasiocarpa*) and Alaska yellow cedar (*Chamaecyparis nootkatensis*) are occasionally present in smaller numbers. Dominant vegetation in clearcuts includes mountain hemlock, Pacific silver fir and Alaska-yellow cedar as regeneration, and big huckleberry (*Vaccinium membranaceum*), Alaska huckleberry, alpine ladyfern (*Athyrium filix-femina*), stink currant (*Ribes bracteosum*), and salmonberry (*Rubus spectabilis*).

## Sampling Design

Soils were studied at four sites where undisturbed, late-successional forest stands abut clearcuts. All sites were selected to maintain similar topography, slope, and tree age class (Table 1). Post-harvest logging residues were previously yarded, piled, and burned at Sites 1 and 2, and only yarded and piled at Sites 3 and 4.

Within each forest and clearcut, three soil pits were excavated to allow sampling and description of the entire soil profile. Soil pits were at 50-m intervals at the same elevation across the slope. Soil pits in clearcuts were at least 50 m from the edge of the adjacent forest canopy. Soil pits were excavated to bedrock or to where rock fragments prohibited further digging. Within each soil profile, one sample was taken from each mineral horizon, and the Oi, Oe, and Oa horizons were composited as one sample, although depths were measured for each O sub-horizon. Additionally, 10 samples of the O horizon were collected at 10-m intervals along the sampling transect to obtain a larger spatial sample than the limited sampling at the soil pits allowed. Litter <2 cm in diameter was collected within a quadrat at each sample point.

## Soil Analysis

Soil chemical analysis included %C, % nitrogen (N), pH, exchangeable cations, CEC, available

TABLE 1. Summary of site characteristics.

| | Site 1 | Site 2 | Site 3 | Site 4 |
|---|---|---|---|---|
| Elevation (m) | 1720 | 1553 | 1355 | 1240 |
| Aspect | S-ESE | N | E-ESE | N-NNW |
| Landform | Valley sidewall | Glacial moraine | Valley sidewall | Valley sidewall |
| Slope (%) | 37 | 48 | 45 | 46 |
| Forest vegetation | | | | |
| Overstory | Pacific silver fir | Pacific silver fir | Pacific silver fir | Mountain hemlock |
| Understory | Moss | Strawberry-leaf | Woody debris | Woody debris |
| | Rustyleaf | huckleberry | Pacific silver fir | Moss |
| | | Alaska huckleberry | | |
| Clearcut vegetation | | | | |
| Regeneration | Alaska yellow cedar | Mountain hemlock | Pacific silver fir | Mountain hemlock |
| | Pacific silver fir | Pacific silver fir | Alaska yellow cedar | Pacific silver fir |
| Understory | Big huckleberry | Salmonberry | Woody debris | Moss |
| | | | Ladyfern | Ladyfern |
| Forest age (yr) | 348 | ≥230 | ≥223 | ≥204 |
| Clearcut year | 1977 | 1964 | 1960 | 1962 |
| Residue treatment | Yard, pile, and burn | Yard, pile, and burn | Yard and pile | Yard and pile |
| Soil subgroup | Typic Haplocryod | Typic Humicryod | Typic Humicryod | Typic Humicryod |
| | | Typic Haplocryod | Typic Haplocryod | Typic Haplocryod |

phosphorus (P), and extractable iron (F) and aluminum (Al). Prior to analysis, all soil samples were air dried and weighed, and mineral soil was sieved through a 2-mm screen.

Organic horizon samples were ground in a Wiley mill with a 20 mesh screen, then subsequently finely ground with a mortar and pestle to ensure homogenization for C and N analysis. Subsamples were analyzed for %C and %N with a CHN analyzer at the Forest Soils Laboratory, University of Washington.

Soluble extractions from the soil subsamples were required for the determination of both exchangeable cations and CEC. Extractions were prepared by saturating 2.5 g of air-dried, < 2-mm mineral soil subsamples with 60 ml of 1.0 M $NH_4OAc$. Samples were then placed in a mechanical extractor overnight to remove $NH_4OAc$ from saturated exchange sites. The resulting solutions were collected and analyzed for exchangeable cation concentration by atomic absorption ($Ca^{2+}$ and $Mg^{2+}$) or atomic emission ($Na^+$ and $K^+$) flame spectrophotometry at the Soil Characterization Laboratory, University of Missouri. Steam distillation and titration were then used to measure the adsorbed $NH_4^+$ and determine CEC (Soil Survey Staff 1992). Base saturation (BS) was calculated as the percent of CEC occupied by exchangeable cations.

Available P was extracted using the Bray 1 absorbed P method (Olsen and Sommers 1982, Soil Survey Staff 1992).

Samples from prospective Bs and Bhs horizons were analyzed for %Fe and %Al to verify spodic criteria (Soil Survey Staff 1992). Two grams of air-dried, < 2-mm soil were saturated with 200 ml of 0.2 M ammonium oxalate. These solutions were mixed on a mechanical shaker for 4 hr in the dark. The solutions were then filtered through a Whatman #42 filter. The resulting filtrates were analyzed for Fe and Al concentrations using inductively coupled argon plasma emission spectroscopy.

Soil pH for each horizon was determined with a pH meter. Deionized water was mixed with <2-mm mineral soil samples (2:1) prior to determination of pH.

Bulk density was determined by extracting an intact soil aggregate from each mineral horizon and measuring its volume displacement in water. Oven-dry mass of each sample soil aggregate was later measured in the laboratory. Bulk density of each horizon was calculated after accounting for the mass and volume of the >2-mm fraction.

Soil C mass (g $kg^{-1}$) for organic horizons was calculated by multiplying C concentration (g $kg^{-1}$) by organic layer mass (kg $m^{-2}$). Soil C mass for mineral soil was calculated as:

$$\begin{aligned} C\ (kg\ m^{-2}) = \Sigma\ [&\text{organic C concentrations of <2-mm material } (g\ kg^{-1}) \\ &\times \text{bulk density of <2-mm material} \\ &\times \text{horizon depth (m)} \\ &\times (1 - \text{rock volume [\%]}/100\%) \\ &\times 10^4\ cm^2\ m^{-2} \times 10^{-6}\ kg^2\ g^{-2}] \end{aligned}$$

where the summation is across the horizons within the soil profile (after Homann et al. 1995). All soil C is organic because carbonates (source of inorganic C) are not found in the parent materials of the study area, and soils are strongly acidic.

### Statistical Analysis

Data were analyzed using an unbalanced, crossed two-factor mixed-effects ANOVA model with replication to detect differences between forests and burned and unburned clearcuts for the following variables: C storage (O horizon and mineral soil), soil chemical properties [pH, CEC, %BS, C, N available P, calcium (Ca), sodium (Na), magnesium (Mg), potassium (K) and C:N], depths in the mineral soil and specifically in spodic horizons, and mineral soil bulk density. Treatment is a fixed effect, and site and interaction are random effects. Correlation analyses were performed between C and all other soil chemical characteristics (N, pH, %B.S., CEC, N, available P and exchangeable cations) in forests, burned clearcuts, and unburned clearcuts. Because horizons varied among soil profiles, comparisons were made between means weighted for differences in horizon mass. Treatment effect differences were considered significant at $P < 0.05$.

## Results

### Soil Profile Characteristics

The cool, moist climate, dominance of coniferous vegetation, and glacial history were the primary influences on pedogenesis in the study area. Relatively shallow soils that have developed since glaciers carved and scoured the study area are on steep slopes prone to movement of hillslope

sediments. Soils at Sites 1, 2, and 4 were primarily sandy loams, while soils at Site 3 were primarily coarse sandy loams (Table 2). An A horizon was absent in all but one clearcut soil profile. Spodosols with strongly expressed E horizons (determined by color) over one or more spodic

TABLE 2. Representative descriptions of forest and clearcut soil profiles at each site. Textures are as follows: C—crumb; CSL—coarse sandy loam; GSL—gravelly sandy loam; LS—loamy sand; SBK—subangular blocky; SL—sandy loam.

| Horizon | Depth (cm) | Color (moist) | Texture | Structure | Rock Volume (%) | Roots |
|---|---|---|---|---|---|---|
| Site 1 Forest, Profile a—Typic Haplocryod | | | | | | |
| O | 1-0 | | | | | |
| E | 0-11 | 10YR 4/2.5 | SL | SBK | 20 | Common medium and fine |
| Bs1 | 11-29 | 7.5YR 3/4 | SL | SBK | 10 | Common medium and fine |
| Bs2 | 29-46 | 7.5YR 3/4 | SL | SBK | 25 | Common medium and fine |
| CB | 46-63 | 7.5YR 2.5/2 | SL | SBK | 40 | Few fine and coarse |
| C | 63+ | | | | | |
| Site 1 Clearcut, Profile b—Typic Haplocryod | | | | | | |
| O | 6-0 | | | | | |
| E | 0-7 | 10YR 5/3 | SL | SBK | 10 | Common fine |
| Bs1 | 7-19 | 7.5YR 4/6 | CSL | SBK | 20 | Common fine; few medium |
| Bs2 | 19-39 | 7.5YR 4/6 | SL | SBK | 10 | Common very fine; few fine |
| CB | 39-62 | 10YR 3/6 | SL | SBK | 50 | none |
| C | 62+ | | | | | |
| Site 2 Forest, Profile c—Typic Haplocryod | | | | | | |
| O | 13-0 | | | | | |
| Eh | 0-5 | 7.5YR 3/2 | SL | SBK | 10 | Few very fine and fine |
| Bhs1 | 5-9 | 5YR 3/3 | SL | SBK | 10 | Few fine and medium |
| Bs2 | 9-21 | 7.5 YR 3.5/5 | SL | SBK | 20 | Few fine |
| Bs3 | 21-32 | 7.5YR 3/4 | SL | SBK | 30 | Few fine and medium |
| BC | 32-52 | 5YR 3/3 | SL | C | 80 | Common fine and medium |
| CB | 52+ | | | | | |
| Site 2 Clearcut, Profile c—Typic Haplocryod | | | | | | |
| O | 2-0 | | | | | |
| 1Bs | 0-11 | 7.5YR 4/4 | SL | SBK | 10 | Common very fine and fine |
| 2E | 11-17 | 7.5YR 3/2.5 | SL | SBK | 5 | Common fine; few medium |
| 2Bs | 17-37 | 7.5YR 3.5/5 | SL | SBK | 10 | Common fine; few medium and coarse |
| 2BC | 37-52 | 10YR 3/3 | GSL | SBK | 20 | Few very fine and fine |
| 2CB | 52-70 | 10YR 2/2 | GSL | SBK | 70 | Few very fine |
| 2C | 70+ | | | | | |
| Site 3 Forest, Profile a—Typic Humicryod | | | | | | |
| O | 2-0 | | | | | |
| Eh | 0-8 | 10YR 4/2 | SL | SBK | 30 | Few fine and coarse |
| Bhs1 | 8-23 | 10YR3/8 | CSL | SBK | 50 | Common coarse |
| Bs2 | 23-45 | 7.5 YR 4.5/6 | SL | SBK | 80 | Few fine; common medium |
| BC | 45-70 | 10YR 3.5/6 | CSL | C | 80 | Few fine and medium |
| CB | 70+ | | | | | |
| Site 3 Clearcut, Profile a—Typic Haplocryod | | | | | | |
| O | 3-0 | | | | | |
| E | 0-7 | 10YR 2/2 | SL | SBK | 5 | Common very fine and fine |
| 1Bs | 7-46 | 7.5YR 3/4 | SL | C | 40 | Common very fine and fine; few medium |
| 2Bs1 | 46-63 | 5YR 3/4 | CSL | C | 20 | Few fine |
| 2Bs2 | 63-77 | 5YR 3.5/5 | CSL | SBK | 40 | Few fine |
| 2BC | 77-94 | 7.5YR 3/4 | CSL | SBK | 90 | none |
| 2CB | 94+ | | | | | |

Continued on next page

TABLE 2. (Continued)

| Horizon | Depth (cm) | Color (moist) | Texture | Structure | Rock Volume (%) | Roots |
|---|---|---|---|---|---|---|
| Site 4 Forest, Profile c—Typic Humicryod | | | | | | |
| O | 8-0 | | | | | |
| Eh | 0-13 | 10YR 2/1 | LS | SBK | 10 | Common fine, medium and coarse |
| Bhs1 | 13-20 | 5YR 3/4 | SL | SBK | 10 | Common fine and medium |
| Bs2 | 20-36 | 10YR 3/3 | LS | SBK | 10 | Few fine and medium |
| Bs3 | 36-64 | 10YR 4/5 | LS | SBK | 10 | Few fine and medium |
| Bs4 | 64+ | 10YR 4/6 | LS | SBK | 20 | Few fine and medium |
| Site 4 Clearcut, Profile c – Typic Humicryod | | | | | | |
| O | 7-0 | | | | | |
| 1Bs1 | 0-10 | 10YR 4/6 | SL | C | 20 | Common very fine; many fine; few medium |
| 1Bs2 | 10-19 | 10YR 3/6 | SL | SBK | 30 | Many fine; few medium |
| 2E | 19-22 | 10YR 3/3 | LS | SBK | 10 | Common fine |
| 2Bs | 22-39 | 7.5YR 3.5/5 | GSL | SBK | 30 | Common fine; few medium |
| 2BC | 39-67 | 10YR 3/6 | GSL | SBK | 50 | Few fine and medium |
| 2C | 67+ | | | | | |

C—crumb; CSL—coarse sandy loam; GSL—gravelly sandy loam; LS—loamy sand; SBK—subangular blocky; SL—sandy loam

horizons (determined by color and Al and Fe content) were a dominant feature. Thick spodic horizons (up to 30 cm) frequently developed immediately above parent materials.

The O horizon was generally thicker in forests than in clearcuts (Table 3), although this difference was not statistically significant due to high variance among soil profiles. Mean proportion of the soil profile comprising spodic horizons was highest for forested sites, followed by clearcuts and burned clearcuts (Table 3), although these differences were not statistically significant. Rock content generally increased from 10% in upper horizons to 50-80% in deeper horizons. Exceptions occurred where movement of hillslope sediments had mixed the soil profile components. There were more buried horizons in clearcuts than forests, which suggests that forest harvest may have encouraged movement of hillslope sediments, although there were no data to confirm this.

## Soil Carbon

Mean C storage in the O horizon was higher for forests than for clearcuts (Table 4), and mean C storage in the mineral soil was less for forests than for clearcuts. Neither difference was statistically significant due to high variance among soil profiles. Carbon storage and concentration in spodic horizons appeared mostly unaffected by tree harvest and burning. Although burned clearcuts had less C than unburned clearcuts, the difference was not significant.

As expected, C concentrations in the mineral soil generally were high (Table 4). Carbon concentrations were typically lowest in BC, CB, and

TABLE 3. Mean (± SE) bulk density, and horizon and soil profile depths for forests and clearcuts.

| Site | Bulk density ($g\ cm^{-3}$) | Horizon depth: O (cm) | Horizon depth: E (proportion of total) | Horizon depth: Bs/Bhs (proportion of total) | Total depth (cm) |
|---|---|---|---|---|---|
| Forest | 0.52 ± 0.07 | 10.2 ± 4.6 | 0.15 ± 0.02 | 0.67 ± 0.10 | 63.8 ± 16.8 |
| All clearcuts | 0.45 ± 0.02 | 5.5 ± 0.8 | 0.10 ± 0.02 | 0.53 ± 0.13 | 75.5 ± 11.1 |
| Burned clearcut | 0.46 ± 0.01 | 5.6 ± 5.9 | 0.09 ± 0.01 | 0.43 ± 0.09 | 67.0 ± 8.0 |
| Unburned clearcut | 0.44 ± 0.03 | 5.3 ± 1.2 | 0.11 ± 0.00 | 0.62 ± 0.04 | 84.0 ± 3.8 |

TABLE 4. Mean (± SE) C storage and concentration for forests and clearcuts.

| Site | O horizon (Mg ha$^{-1}$) | Mineral soil: All horizons (Mg ha$^{-1}$) | Mineral soil: All horizons (g kg$^{-1}$) | Mineral soil: Bs/Bhs horizons (g kg$^{-1}$) |
|---|---|---|---|---|
| Forest | 48.8 ± 16.1 | 95.4 ± 51.7 | 51.0 ± 19.3 | 49.5 ± 15.0 |
| All clearcuts | 30.0 ± 21.2 | 131.3 ± 46.0 | 50.2 ± 7.0 | 45.3 ± 8.7 |
| Burned clearcut | 29.5 ± 36.5 | 114.2 ± 29.8 | 45.1 ± 11.0 | 39.9 ± 5.2 |
| Unburned clearcut | 30.6 ± 4.5 | 148.4 ± 65.5 | 55.3 ± 2.6 | 50.7 ± 9.0 |

C horizons when those horizons were present, however, there was no consistent pattern in the spatial distribution of C in the overlying horizons.

## Soil Chemical Characteristics

Post-harvest changes in soil chemical characteristics appeared to be at least partially controlled by logging residue treatment and were often correlated with C concentrations (Tables 5, 6). Calcium concentration was significantly higher in mineral soils of clearcuts than in uncut forests, with unburned clearcuts having the highest Ca concentration (Table 5). However, most other cations and soil chemical properties were similar between clearcuts and forests and between burned and unburned clearcuts. Nitrogen concentrations in the mineral soil were mostly unaffected by cutting and burning treatments.

Several soil chemical properties were correlated with C concentrations in this study (Table 6), although correlations were not consistent among forest vs. clearcut and burned vs. unburned clearcuts. One of the strongest correlations we discovered between C and N concentrations was significant for burned clearcuts only. There was also a significant correlation between C and CEC and between C and BS, but only for the two clearcut treatments.

TABLE 5. Mean (± SE) chemical properties of mineral soil for forests and clearcuts.

| Site | pH ($H_2O$) | CEC (cmol kg$^{-1}$) | B.S. (%) | N (g kg$^{-1}$) | Avail. P (mg kg$^{-1}$) | Ca (mg kg$^{-1}$) | Mg (mg kg$^{-1}$) | Na (mg kg$^{-1}$) | K (mg kg$^{-1}$) | C:N |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | All horizons | | | | | |
| Forest | – | 35.1 ± 10.7 | 2.0 ± 0.7 | 1.7 ± 0.6 | 4.1 ± 3.0 | 61 ± 37 | 1.1 ± 0.6 | 19.4 ± 2.0 | 29.5 ± 2.7 | 30.1 ± 4.9 |
| All clearcuts | – | 31.6 ± 6.2 | 5.1 ± 3.0 | 1.5 ± 0.6 | 6.0 ± 4.1 | 271 ± 177 | 1.2 ± 1.0 | 17.7 ± 2.2 | 28.4 ± 7.9 | 37.5 ± 13.1 |
| Burned clearcut | – | 30.6 ± 5.9 | 2.6 ± 0.7 | 1.1 ± 0.6 | 6.6 ± 6.4 | 128 ± 57 | 0.5 ± 0.3 | 16.2 ± 1.8 | 24.7 ± 6.5 | 46.1 ± 16.0 |
| Unburned clearcut | – | 32.4 ± 8.9 | 7.6 ± 0.4 | 1.9 ± 0.3 | 5.5 ± 2.7 | 415 ± 94 | 1.9 ± 1.1 | 19.5 ± 0.4 | 32.2 ± 9.4 | 29.0 ± 5.5 |
| | | | | | Bs/Bhs horizons | | | | | |
| Forest | 4.4 ± 0.3 | 39.3 ± 7.3 | 1.9 ± 0.8 | 1.7 ± 0.6 | 3.9 ± 2.7 | 45 ± 22 | 0.9 ± 0.7 | 18.5 ± 2.1 | 29.6 ± 6.8 | 30.6 ± 7.9 |
| All clearcuts | 4.9 ± 0.2 | 33.2 ± 7.2 | 5.4 ± 3.3 | 1.4 ± 0.5 | 2.6 ± 0.7 | 183 ± 102 | 1.8 ± 1.8 | 19.1 ± 3.2 | 28.4 ± 7.4 | 36.3 ± 12.7 |
| Burned clearcut | 4.4 ± 0.6 | 33.4 ± 9.7 | 3.5 ± 3.2 | 0.9 ± 0.1 | 2.3 ± 0.9 | 108 ± 91 | 2.1 ± 3.0 | 18.2 ± 4.7 | 29.7 ± 12.1 | 44.9 ± 12.2 |
| Unburned clearcut | 4.6 ± 0.2 | 33.1 ± 7.8 | 7.3 ± 2.8 | 1.8 ± 0.0 | 3.0 ± 0.1 | 257 ± 25 | 1.6 ± 1.1 | 20.0 ± 2.1 | 27.1 ± 3.7 | 27.7 ± 6.4 |

TABLE 6. Significant correlation coefficients ($r^2$) between C concentration and soil chemical properties in forests, burned clearcuts, and unburned clearcuts. No correlations were significant for pH, Na, and K.

| | CEC (cmol kg$^{-1}$) | B.S. (%) | N (g kg$^{-1}$) | Available P (mg kg$^{-1}$) | Ca (mg kg$^{-1}$) | Mg (mg kg$^{-1}$) |
|---|---|---|---|---|---|---|
| Forest | — | — | — | 0.20 | — | 0.31 |
| Burned clearcut | 0.80 | 0.22 | 0.80 | 0.27 | — | — |
| Unburned clearcut | 0.23 | 0.25 | — | — | 0.33 | 0.24 |

## Discussion

We identified a possible trend toward decreased O-horizon depth after timber harvest (Table 3). Previous studies have attributed decreases in O-horizon accumulations after harvest (without burning) to: (1) redistribution of residues into the mineral soil at the time of clearcutting, (2) ensuing decomposition (Johnson et al. 1991, Ryan et al. 1992, Black and Harden 1995, Parker et al. 2001) and (3) the post-harvest dominance of herbaceous and deciduous litter that decomposes more easily than coniferous litter (Edmonds 1980).

The amount of the soil profile comprising spodic horizons was not significantly different in clearcuts than in uncut forests (Table 3). In a study of Spodosols in deciduous hardwood clearcuts in New Hampshire, thicker Bs1 horizons observed 3 yr after timber harvest were due to increased solubility and mobility of soil organic matter (Johnson et al. 1991). However, it is also possible that in coniferous forests spodic characteristics break down after tree harvest due to the loss of organic acids from overstory trees (R. David Hammer, University of Missouri, personal communication).

Although forests may be more productive and have slower decomposition rates than young regeneration in clearcuts (Covington 1981), logging residues in cool coniferous ecosystems persist for long periods of time (Harmon et al. 1990, Johnson and Curtis 2001) and probably contribute to the similar quantities of O-horizon C in forests and clearcuts in this study. A large portion of the soil C in late-successional forests is stored as lignin (Entry and Emmingham 1998), which reduces organic matter decomposition and C turnover rates and facilitates high C concentrations. Much of the primary source of soil C (surficial organic matter and logging residues) was oxidized when burning was conducted following clearcut logging. Consequently, easily decomposed herbaceous litter (relative to the forest) has been the primary source of soil C since harvest in burned clearcuts.

Immediately after harvest, C storage in the O horizon may change depending upon how the severity of the disturbance at the time of harvest affects the quality and quantity of logging residues (Johnson 1992, Piatek and Allen 1999, Harmon and Marks 2002). Eventually a period is reached when organic matter degrades as wood and leaf litterfall are reduced by tree removal, and residues left on site decompose (Covington 1981, Parker et al. 2001). The degradation phase may be augmented by higher decomposition rates (Marra and Edmonds 1996, MacDonald et al. 1999) and the prevalence of herbaceous and shrub litter that decomposes relatively quickly. The degradation phase gradually shifts to an aggradation phase as vegetation recovers and the quantity and size of wood litterfall increases (Covington 1981).

The clearcuts in this study appear to be in the degradation phase. O-horizon C storage was likely greater in clearcuts than in forests immediately after harvest due to logging inputs (Johnson et al. 1991, Simard et al. 2001, Bock and Van Rees 2002). Although there may be some release of C from decomposing logging residues, the similarity in O-horizon C between forests and clearcuts indicates that C inputs from decomposing logging residues are probably decreasing. The translocation of C from decomposing logging residues and accelerated decomposition of litter from early successional plants can increase soil C pools in unburned clearcuts (Covington 1981, Johnson et al. 1991, Entry and Emmingham 1998, Bock and Van Rees 2002).

The similar C concentrations between forests and clearcuts in this study, however, indicate another mechanism may be at work. For example, total C storage can be affected simply by differences in soil volume among soil profiles. In addition, movement of hillslope sediments can transport C deeper into the soil profile and result in large reserves of long-term C storage (Richter et al. 1995, Christensen et al. 1999), especially in mountain landscapes.

Effects of timber harvest on mineral-soil C pools tend to be relatively small in most forests, with net gains or losses affected mostly by the type of residue management (Johnson 1992). No difference was found in the top 10 cm of burned and unburned mineral soils 32-36 yr after broadcast burn in the western Cascade Range in Oregon and Washington (Kraemer and Hermann 1979). In a study evaluating the effects of post-harvest residue removal, no detectable differences were found in mineral soil C storage 5 mo after tree harvests in a southern mixed deciduous forest (Edwards and Ross-Todd 1983). No change in mineral soil C pools were found in northern hardwood forests 3 yr after harvest, although there was evidence of redistribution of organic matter in the solum (Johnson et al. 1991).

With the notable exception of Ca, we found minimal changes in other soil chemical properties that might have been affected by cutting and burning. At 20-40 yr after harvest and burning, any nutrients that were initially released have likely been removed through leaching in this high-precipitation environment. A variety of effects on soil chemistry have been observed at different temporal scales in other forests. Soil pH, N, CEC, Ca, and Mg increased, and K decreased after clearcutting a boreal mixed-wood forest (Bock and Van Rees 2002). Large post-harvest (without burning) changes in exchangeable cations in forest soils in the southeastern U.S. have been attributed to plant uptake and leaching (Johnson and Todd 1990, Knoepp and Swank 1994, Richter et al. 1995). Studies of mineral soils in forests within 2 yr after burning found increases in soil nutrients, which, except for N, were largely retained in the soil (Adams and Boyle 1980).

High post-harvest Ca concentrations in the mineral component of subalpine soils may have been related to the stability of Ca cations. Soil organic matter typically selects for divalent over monovalent cations, and Ca moves through the soil with anions released as organic matter mineralizes (Snyder and Harter 1984). This is a potentially important change in chemical cycling, because these subalpine soils have very low cation content. Increased residence time of Ca may be particularly important in Spodosols in which Ca tends to accumulate in spodic horizons after tree harvest (Snyder and Harter 1984; Johnson et al. 1991, 1995, 1997). Calcium in the mineral soil may eventually return to pre-harvest levels as it is accumulated by recovering forest vegetation (Knoepp and Swank 1994, Richter et al. 1995). Positive correlations between C and CEC and between C and exchangeable cations found in this study are typical in Spodosols with low clay contents (Federer 1984, Federer and Hornbeck 1985, Johnson et al. 1995).

At 20-40 yr after harvest, similar O-horizon C pools and mineral soil C concentrations in forests and clearcuts indicate that a mechanism other than logging residue decomposition and mixing into the mineral soil may be responsible for current patterns. Buried horizons in clearcuts indicate that deeper soils may be the result of harvest-induced movement of hillslope sediments. Consequently C storage likely varies spatially within the clearcuts. Organic matter is an important source of exchange sites for soil nutrients in these low-clay Spodosols, and logging slash continues to be a source of soil nutrients, particularly Ca, up to 40 yr after clearcutting. The soil environment should be a strong consideration in management of subalpine forests of the Cascade Range, particularly with respect to treatment of logging residues, because post-harvest effects may require decades to be fully manifested.

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## Literature Cited

Adams, P. W., and J. R. Boyle. 1980. Effects of forest fire on soil nutrients in clearcut and whole-tree harvest sites in central Michigan. Soil Science Society of America Journal 44:847-850.

Alban, D. H., and D. A. Perala. 1992. Carbon storage in Lake States aspen ecosystems. Canadian Journal of Forest Research 22:1107-1110.

Black, T. A., and J. W. Harden. 1995. Effect of timber harvest on soil carbon storage at Blodgett Experimental Forest, California. Canadian Journal of Forest Research 25:1385-1396.

Bock, M. D., and K. C. J. Van Rees. 2002. Forest harvesting impacts on soil properties and vegetation communities in the Northwest Territories. Canadian Journal of Forest Research 32:713-724.

Borchers, J. G., and D. A. Perry. 1992. The influence of soil texture and aggregation on carbon and nitrogen dynamics in southwest Oregon forests and clearcuts. Canadian Journal of Forest Research 22:298-305.

Burger, J. A., and W. L. Pritchett. 1984. Effects of clearfelling and site preparation on nitrogen mineralization in a southern pine stand. Soil Science Society of America Journal 48:1432-1437.

Christensen, T. R., S. Johnson, T. V. Callaghan, and M. Havstrom. 1999. On the potential $CO_2$ release from tundra soils in a changing climate. Applied Soil Ecology 11: 127-134.

Covington, W. W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. Ecology 62:41-48.

Edmonds, R. L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. Canadian Journal of Forest Research 10: 327-337.

Edwards, N. T., and B. M. Ross-Todd. 1983. Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residue removal. Soil Science Society of America Journal 47:1014-1021.

Entry, J. A., and W. H. Emmingham. 1998. Influence of forest age on forms of carbon in Douglas-fir soils in the Oregon Coast Range. Canadian Journal of Forest Research 28:390-395.

Federer, C. A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. Canadian Journal of Forest Research 14:763-767.

Federer, C. A., and J. W. Hornbeck. 1985. The buffer capacity of forest soils in New England. Water Air Soil Pollution 26:163-173.

Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and belowground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Canadian Journal of Forest Research 11: 155-167.

Harmon, M. E., and B. Marks. 2002. Effects of silvicultural practices on carbon stores in Douglas-fir – western hemlock forests in the Pacific Northwest, U.S.A.: results from a simulation model. Canadian Journal of Forest Research 32:863-877.

Harmon M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects of carbon storage of conversion of old-growth forests to young forests. Science 247:699-702.

Homann, P. S., P. Sollins, H. N. Chappell, and A. G. Stangenberger. 1995. Soil organic carbon in a mountainous, forested region: relation to site characteristics. Soil Science Society of America Journal 59: 1468-1475.

Johnson, C. E., A. H. Johnson, T. G. Huntington, and T. G. Siccama. 1991. Whole-tree clear-cutting effects on soil horizons and organic-matter pools. Soil Science Society of America Journal 55:497-502.

Johnson, C. E., C. T. Driscoll, T. J. Fahey, T. G. Siccama, and J. W. Hughes. 1995. Carbon dynamics following clear-cutting of a northern hardwood forest. Pages 463-486 *In* W. W. McFee and J. M. Kelly (editors), Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Madison, Wisconsin.

Johnson, C. E., R. B. Romanowicz, and T. G. Siccama. 1997. Conservation of exchangeable cations after clear-cutting of a northern hardwood forest. Canadian Journal of Forest Research 27:859-868.

Johnson, D. W. 1992. Effects of forest management on soil carbon storage. Water, Air, and Soil Pollution 64:83-120.

Johnson, D. W., and P. S. Curtis. 2001. Effects of forest management on soil C and N: storage meta analysis. Forest Ecology and Management 40:227-238.

Johnson, D. W., D. W. Cole, C. S. Bledsoe, K. Cromack, Jr., R. L. Edmonds, S. P. Gessel, C. C. Grier, B. N. Richards, and K. A. Vogt. 1982. Nutrient cycling in forests of the Pacific Northwest. Pages 186-232 *In* R. L. Edmonds (editor), Analysis of Coniferous Forest Ecosystems in the Western United States. Hutchinson Ross, Stroudsberg, Pennsylvania.

Johnson, D. W., and D. E. Todd. 1990. Nutrient cycling in forests of Walker Branch Watershed, Tennessee: roles of uptake and leaching in causing soil changes. Journal of Environmental Quality 19:97-104.

Johnson, D. W., and D. E. Todd. 1998. Effects of harvesting intensity on forest productivity and soil carbon storage in a mixed oak forest. Pages 351-363 *In* R. Lal, J. M. Kimble, R. F. Follett, and B. A. Stewart (editors), Management of Carbon Sequestration in Soil. CRC Press, Boca Raton, Florida.

Kirschbaum, M. U. F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27:753-760.

Knoepp, J. D., and W. T. Swank. 1994. Long term soil chemistry changes in aggrading forest ecosystems. Soil Science Society of America Journal 58:325-331.

Knoepp, J. D., and W.T. Swank. 1997. Forest management effects on surface soil carbon and nitrogen. Soil Science Society of America Journal 61:928-935.

Kraemer, J. F., and R. K. Hermann. 1979. Broadcast burning prescribed fire: 25-year effects on forest soils in the western flanks of the Cascade Mountains. Forest Science 25:427-439.

Kuramoto, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs 40:317-347.

MacDonald, N. W., D. L. Randlett, and D. R. Zak. 1999. Soil warming and carbon loss from a lake states spodosol. Soil Science Society of America Journal 63:211-218.

Marra, J. L., and R. L. Edmonds. 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A.. Canadian Journal of Forest Research 26:1337-1345.

Mattson, K. G., and W. T. Swank. 1989. Soil and detrital carbon dynamics following forest cutting in the Southern Appalachians. Biology and Fertility of Soils 7:247-253.

Miller, J. H., and D. L. Sirois. 1986. Soil disturbance by skyline yarding vs. skidding in a loamy hill forest. Soil Science Society of America Journal 50:1579-1583.

Olsen, S. R., and L. E. Sommers. 1982. Phosphorus. Pages 403-430 *In* A. L. Page, R. H. Miller, and D.R, Keeney (editors), Methods of Soil Analysis, Part 2: Chemical and Microbiological Properties. American Society of Agronomy, Madison, Wisconsin.

Parker, J. L., I. J. Fernandez, L. E. Rustad, and S. A. Norton. 2001. Effects of nitrogen enrichment, wildfire, and harvesting on forest-soil carbon and nitrogen. Soil Science Society of America Journal 65:1248-1255.

Piatek, K. B., and H. L. Allen. 1999. Nitrogen mineralization in a pine plantation fifteen years after harvesting and site preparation. Soil Science Society of America Journal 63:990-998.

Powers, R. F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. Soil Science Society of America Journal 44:1314-1320.

Powers, R. F., and K. Van Cleve. 1991. Long-term ecological research in temperate and boreal forest ecosystems. Agronomy Journal 83:11-24.

Prichard, S. J., D. L. Peterson, and R. D. Hammer. 2000. Carbon distribution in subalpine forests and meadows of the Olympic Mountains, Washington. Soil Science Society of America Journal 64:1834-1845.

Richter, D. D., D. Markewitz, C. G. Wells, H. L. Allen, J. K. Dunscombe, K. Harrison, P. R. Heine, A. Stuanes, B. Urrego, and G. Bonan. 1995. Carbon cycling in a loblolly pine forest: implications for the missing carbon sink and for the concept of soil. Pages 233-252 *In* W.W. McFee and J.M. Kelly (editors), Carbon Forms and Functions in Forest Soils, Soil Science Society of America, Madison, Wisconsin.

Rustad, L. E., and I. J. Fernandez. 1998. Soil warming: consequences for foliar litter decay in a spruce-fir forest in Maine, USA. Soil Science Society of America Journal 62:1072-1080.

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Ryan, D. F., T. G. Huntington, and C. W. Martin. 1992. Redistribution of soil nitrogen, carbon and organic matter by mechanical disturbance during whole-tree harvesting in northern hardwoods. Forest Ecology and Management 49:87-99.

Simard, D. G., J. W. Fyles, D. Paré, and T. Nguyen. 2001. Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. Canadian Journal of Soil Science 81:229-237.

Snyder, K. E., and R. D. Harter. 1984. Changes in solum chemistry following clearcutting of northern hardwood stands. Soil Science Society of America Journal 49:223-228.

Soil Survey Staff. 1992. Soil Survey Lab Methods Manual. Soil survey investigations report 42. USDA Soil Conservation Service, Lincoln, Nebraska.

Soil Survey Staff. 1999. Keys to Soil Taxonomy, 9th edition. Pocahontas Press, Blacksburg, Virginia.

Stone, E. L., W. G. Harris, R. B. Brown, and R. J. Kuehl. 1993. Carbon storage in Florida spodosols. Soil Science Society of America Journal 57: 179-182.

Vogt, K. A., E, Moore, S. Gower, D. Vogt, D. Sprugel, and C. Grier. 1989. Productivity of upper slope forests in the Pacific Northwest. Pages 137-163 *In* D. Perry (editor), Maintaining the Long-term Productivity of Pacific Northwest Ecosystems. Timber Press, Portland, Oregon.

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# The Influence of Thinning on Production of Hypogeous Fungus Sporocarps in Douglas-fir Forests in the Northern Oregon Coast Range

## Abstract

Sporocarps of hypogeous fungi are an important food resource for many wildlife species. Effects of thinning second-growth (35 to 45 yr-old) Douglas-fir forests on production of hypogeous sporocarps were investigated to test the hypothesis that in the short term thinning would reduce their production and species diversity. We compared sporocarp production among unthinned, moderately thinned, and heavily thinned stands in four locations in the Oregon Coast Range, 1996 and 1997. Distributions of hypogeous sporocarps were clumped. Total biomass of sporocarps was highest in spring 1996 and progressively decreased in subsequent sampling periods. The genera *Alpova, Barssia, Elaphomyces, Truncocolumella,* and *Tuber* appeared to decrease in response to thinning. Thinning significantly reduced total sporocarp frequency among treatments. The mean number of species fruiting was significantly higher in the unthinned than thinned treatments, and more species occurred in the unthinned than thinned treatments in autumn 1996. The array of sporocarp-producing species varied between treatments. Sporocarp distributions were clumped at the plot and grid station levels, and total sporocarp abundance was associated with abundance of coarse woody debris (CWD). These results indicated that commercial thinning influenced hypogeous sporocarp production and sporocarp species diversity at 2 to 3 yr after cutting and that CWD was an important variable for predicting hypogeous sporocarp production. Retention of CWD in commercially thinned sites seems important for sporocarp production of certain hypogeous species and thus to habitat maintenance for many small mammal mycophagists.

## Introduction

Hypogeous fungi play important roles in many forest ecosystems. They form mycorrhizae with many trees and shrubs, which depend on them for uptake of nutrients and water; the plant hosts provide photosynthates to the fungi (Read et al. 1992). The sporocarps are an important food source for many small mammal species in the Pacific Northwest, including California red-backed voles (*Clethrionomys californicus*) (Maser et al. 1978, Ure and Maser 1982), northern flying squirrels (*Glaucomys sabrinus*) (Maser and Trappe 1984, Maser et al. 1985, Carey et al. 2002), and wood rats (*Neotoma* spp.) (Parks 1919, Maser et al. 1978). Small mammal mycophagy in turn acts as the primary means of spore dispersal for these fungi (Fogel and Trappe 1978).

Hypogeous sporocarp formation differs in productivity and species diversity in forests of different ages and habitats. Sporocarp production can be higher in mature conifer stands than in young stands and species composition can differ between the stands (Vogt et al. 1981). This may relate to photosynthetic potential, which is positively correlated with abundance of ectomycorrhizal fungal sporocarps in forests (Termorshuizen and Schaffers 1987). Luoma et al. (1991) compared hypogeous fungal production along moisture and age gradients in Douglas-fir forests in the Oregon Cascades. Biomass was highest in the mesic mature habitats, followed by mesic old-growth, mesic young, wet old-growth, and dry old-growth habitats.

Other researchers have evaluated effects of silvicultural practices on species diversity and sporocarp production. More hypogeous sporocarps occurred in mature stands than in adjacent, regenerated clearcuts, and sporocarp abundance was associated with the presence of coarse woody debris (CWD) in the studies of Amaranthus et al. (1994) and Clarkson and Mills (1994). Colgan et al. (1999) sampled hypogeous sporocarp production at 6-wk intervals over 34 mo after a variable density thinning of Douglas-fir (*Pseudotsuga*

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*menziesii*) in lowland western Washington. Overall standing crop biomass was significantly lower in the thinned stands compared with unthinned. Some taxa of hypogeous fungi fruited less abundantly in thinned than unthinned stands, and others were more abundant in thinned stands. Waters et al. (1994) evaluated sporocarp standing crop biomass 9 and 10 yr after two levels of commercial thinning and 17 yr after broadcast burning. Thinning did not significantly affect hypogeous sporocarp biomass or frequency, but the fungal community composition differed between levels of thinning. Sporocarp standing crop also varies seasonally and is affected by climate (Fogel 1981, Eveling et al. 1990) and sporocarp moisture content (Johnson 1994), so assessing the overall impact of thinning can be difficult.

The positive association of sporocarp abundance with the presence of CWD can affect the presence of mycophagists in an area, because they are attracted to the sporocarps as a food source. California red-backed voles represent fungal specialists strongly associated with CWD (Maser et al. 1978, Ure and Maser 1982, Maser 1998). Small mammal mycophagists rely on a diversity of fungal species in their diets (Maser et al. 1978, 1985, Carey et al. 2002). This diversity may be a nutritional imperative, as suggested in feeding trials with northern flying squirrels and California red-backed voles, where neither species maintained their body weight on a single species of fungi (Claridge et al. 1999).

Because hypogeous fungal sporocarps are important as food for small mammals in Pacific Northwest forests, management of habitat for those mammals and their predators requires knowledge of how forest management practices affect sporocarp production. Accordingly, we compared sporocarp production of hypogeous fungi among moderately and heavily thinned and unthinned stands in blocks at four locations in second-growth forests in the Oregon Coast Range. We hypothesized that thinning would negatively affect sporocarp production and diversity of sporocarp-producing fungi in the short run, because ectomycorrhizal fungi depend on hosts plants for photosynthates (Molina et al. 1992, Read et al. 1992), and mycorrhizae tend to be concentrated in the upper mineral and organic layers most susceptible to disturbance during timber harvest (Waters et al. 1994).

## Methods

### Study Area

The study was located in the northern Oregon Coast Range ~14 km WNW of Forest Grove on Tillamook State Forest and adjacent Stimson Lumber Company lands, Tillamook and Washington Counties, Oregon. The area was chosen for its large acreage of even-aged, closed-canopy, fire-replacement forest. In addition, most of the landscape is dominated by contiguous forest habitat, thus reducing potential confounding influences of forest fragmentation on stand-level phenomena. Douglas-fir was the dominant tree species; red alder (*Alnus rubra*) occupied riparian and recently disturbed areas. Less common trees included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and noble fir (*Abies procera*). Vine maple (*Acer circinatum*) and red huckleberry (*Vaccinium parvifolium*) were dominant deciduous shrubs, and salal (*Gaultheria shallon*) and Oregon grape (*Berberis nervosa*) were the most common evergreen shrubs. This area has a maritime climate, with mild, wet winters and cool, dry summers (Brown and Curtis 1985).

### Sampling Design

We established four replicate blocks, each initially consisting of three 35- to 45 yr-old unthinned 26-40 ha stands. Stands within blocks were <0.5 km apart, with the exception of one in the Deer Diamond block, which was ca. 1.5 km from the other stands. Blocks were selected to minimize differences among stands within blocks with respect to tree density, stand age, and proportion of hardwoods. One of three treatments was randomly assigned to each of the three stands in each block: 1) no thinning (455-680 trees/ha), 2) moderate thinning (240-330 trees/ha) and, 3) heavy thinning (165-240 trees/ha). Stands were thinned in summer and autumn 1994 following one season of pre-treatment sampling.

Grids with 40 m between sampling stations were established in each stand. Grid arrays varied from 17 X 6 to 10 X 10 with 96-100 stations, depending on size and shape of the stand. Each grid had at least 20 m between its perimeter and the edge of the stand.

### Habitat and Fungal Sampling

Habitat characteristics, measured in 10-m radius plots centered at every fourth grid station, included live trees, snags, stumps, CWD, and slash. Species, diameter at breast height (dbh) and height were recorded for all live trees ≥ 2-m tall and ≥ 10 cm dbh. Stumps ≥ 20-cm diameter and < 2-m tall were tallied, CWD ≥ 1-m long and ≥ 10-cm in diameter were recorded by size class, and the dimensions of each slash pile (width, length, and height) were estimated. Plots of 20-m radius were established to record dbh, height, and decay class (Maser and Trappe 1984) of each snag ≥ 2-m high and ≥ 10 cm dbh.

Hypogeous fungal sporocarps were sampled in late April–early June and October–early November of 1996 and again in late April–June of 1997 on 4-$m^2$ circular plots located at a random distance between 1 and 20 m from every fourth station on each grid. In autumn 1996 and spring 1997 we located a new sample point 180° from the point originally sampled. Litter was removed and topsoil raked to a depth of 5-10 cm as described by Luoma et al. (1991). All sporocarps were collected, dried, weighed, and identified to genus and, when mature enough, species. Voucher specimens were deposited in the Mycological Herbarium at Oregon State University, Corvallis, Oregon (OSC).

### Statistical Analyses

Hypogeous species of the same genus were combined for analysis of standing crop biomass because sample sizes were small for several species and some juvenile specimens were identifiable only to genus. Individual species were used for testing relationships of measured variables to diversity of sporocarp producers: immature specimens could be separated by species in the absences of mature spores through combinations of other characters, even though a species name could not be applied. Differences among treatments were tested for habitat variables, standing crop biomass (dry weight) and percent frequency of sporocarps among treatments and blocks for the five most common genera of hypogeous fungi by ANOVA for a randomized block design. By the same approach total biomass, total frequency, and number of genera were compared among treatments within sample periods. Repeated measures analysis was used to compare total biomass, frequency (percentage of plots where hypogeous sporocarps were found), and number of genera among treatments, with sample period used as the repeated factor. Variables were $\log_{10}(x+1)$ or square-root transformed to adjust for non-normality or lack of homogeneity of variances. Differences in fungal sporocarp associations among treatments were compared by Chi-square goodness-of-fit tests. Number of sporocarps per plot and collections per grid station were compared to numbers expected based on the Poisson distribution (Steele and Torre 1980) by Chi-square analysis. We tested each season by treatment separately at the plot level, because Chi-square tests indicated significant association between treatment and number of sporocarps per plot. Each site was tested separately at the grid station level, because of significant association between site and number of sporocarp collections per grid station. We also conducted pooled analysis across season, site, and treatment.

Associations of sporocarps to habitat characteristics were tested with multiple linear regression (separate analysis by genus was possible only for the most abundant genera). We present the best model chosen from the top ten given by Mallows $C_p$ selection criteria (Mallows 1973) based on the biological significance of the independent variables and the amount of explained variability in the model. The level of significance for all statistical tests was set at $P$=0.05.

## Results

### Habitat Characteristics

Canopy cover of small conifers ($P$<0.001), total tree cover ($P$<0.001), and abundance of small snags ($P$<0.02) and all snags ($P$<0.03) were significantly higher in unthinned stands than in thinned stands (Table 1). Stump abundance was significantly greater in thinned stands than unthinned ($P$<0.001), and slash was greater in the thinned stands than unthinned ($P$=0.001 for heavy thinning, $P$=0.002 for moderate thinning).

### *Hypogeous sporocarp diversity and abundance*

In all, 3576 $m^2$ were sampled. Hypogeous sporocarps were found in 68 (17%) of the 894 plots. The 566 sporocarps collected totaled 106.2 g dry weight and 0.3 kg/ha standing crop biomass. The

TABLE 1. Mean stand characteristics of 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, Spring 1996 and 1997 and Autumn 1996. Means computed from mean of subsamples within each stand (n = 22-34). Variables were $\log_{10}(x + 1)$ transformed.

| Variable | Treatment: Unthinned (n=4) | Moderate Thinning (n=4) | Heavy Thinning (n=4) | *P* Value |
|---|---|---|---|---|
| Deciduous trees 10-49 cm dbh: no./ha. | 33.4 ± 12.1 | 29.9 ± 14.3 | 37.9 ± 7.3 | 0.884 |
| Deciduous trees ≥ 50 cm dbh: no./ha. | 0.6 ± 0.3 | 1.6 ± 1.6 | 0.3 ± 0.3 | 0.601 |
| Conifer trees 10-49 cm dbh: no./ha. | 506.1 ± 54.4 | 229.2 ± 22.9 | 145.1 ± 7.0 | 0.001 |
| Conifer trees ≥ 50 cm dbh: no./ha. | 36.3 ± 2.9 | 24.5 ± 9.2 | 20.1 ± 7.6 | 0.530 |
| Total trees: no./ha. | 576.8 ± 45.8 | 285.2 ± 16.2 | 203.1 ± 10.8 | 0.001 |
| Small snags 10-49 cm dbh: no./ha. | 54.6 ± 11.9 | 20.9 ± 4.8 | 13.7 ± 3.2 | 0.011 |
| Large snags ≥ 50 cm dbh: no./ha. | 9.0 ± 4.0 | 3.5 ± 1.4 | 4.7 ± 1.5 | 0.223 |
| Total snags: no./ha. | 63.7 ± 15.5 | 24.4 ± 5.9 | 18.4 ± 4.6 | 0.026 |
| Stumps ≥ 20 cm diam < 2m ht: no./ha. | 81.2 ± 11.5 | 316.7 ± 15.6 | 338.7 ± 35.0 | 0.001 |
| Small logs 10-49 cm diam: no./ha. | 131.1 ± 12.7 | 169.7 ± 35.6 | 195.4 ± 36.9 | 0.321 |
| Large logs ≥ 50 cm diam: no./ha. | 135.3 ± 19.4 | 137.5 ± 4.5 | 154.7 ± 20.4 | 0.469 |
| Total logs: no./ha. | 266.4 ± 25.5 | 306.8 ± 32.5 | 346.9 ± 35.6 | 0.367 |
| Slash: $m^3$/ha. | 6.7 ± 5.4 | 331.0 ± 106.9 | 648.4 ± 378.8 | 0.001 |

20 genera and 34 species included 4 undescribed species (Table 2). Fourteen species were Ascomycetes, 17 Basidiomycetes, 1 Glomeromycetes, and 2 Zygomycetes. *Hysterangium* (33%) and *Rhizopogon* (23%) spp. together accounted for ca. 56% of the total sporocarp biomass (Tables 3 and 4). *Rhizopogon* and *Alpova* spp. produced their highest standing crop biomass in autumn 1996 and *Hysterangium* and *Gautieria* spp. in spring 1997 (Table 4). *Hysterangium* spp. occurred on 24% of the plots with sporocarps, and *Rhizopogon* and *Tuber* each on 18% (Table 3). *Tuber* spp. were collected in more of the stands (92%) than any other genus, followed by *Rhizopogon* (75%) and *Hysterangium* (67%). Total biomass of sporocarps was highest in spring 1996 and progressively decreased in subsequent sampling periods (Table 4). Sporocarps biomass of *Hysterangium, Barssia,* and *Endogone* spp. was higher in spring than autumn. *Gautieria* and *Leucangium* occurred exclusively in spring, whereas *Alpova, Truncocolumella,* and *Geopora* fruited only in autumn (Table 4).

Fruiting of several genera appeared to decrease in response to thinning, including *Alpova, Barssia, Elaphomyces, Truncocolumella,* and *Tuber* (Figure 1A); however, species in these genera were of low abundance, so the power of statistical tests was minimal. Mean hypogeous sporocarp biomass did not differ significantly among treatments for any of the five more common genera (Table 5). Mean total standing crop biomass did not differ significantly among treatments (Figure 1B) or sample periods. Thinning did not significantly affect total sporocarp frequency among treatments or sample periods (Figure 1C).

The mean number of sporocarp-producing species was significantly higher in the unthinned than thinned treatments ($P<0.05$, Figure 2), and more species fruited in the unthinned than thinned treatments in autumn 1996 ($P<0.04$). The overall mean of fruiting species did not differ significantly among sample periods.

The array of taxa fruiting varied between treatments (Figure 3), but number of collections of sporocarps was not significantly associated with level of thinning. This analysis could only be completed for *Hysterangium, Rhizopogon*, and *Tuber*, because the small sample sizes for the other species produced expected cell frequencies <5 in the analysis.

### *Hypogeous sporocarp distribution*

More hypogeous sporocarps occurred per plot in unthinned than thinned stands ($P=0.04$, Figure 4A), and more sporocarps were found per grid station (n=3 sample plots or periods per station or grid point) in unthinned than thinned stands (Figure 4B). Sporocarps were not randomly dis-

TABLE 2. Taxa of hypogeous fungi collected in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, Spring 1996 and 1997 (S) and Autumn 1996 (A). Numbers after each species name refer to collections deposited in the Mycological Herbarium of Oregon State University, Corvallis (OSC).

**Ascomycota**

*Barssia oregonensis* (S, A): Trappe 22765
*Elaphomyces granulatus* (S): Trappe 22724
*Genea intermedia* (S): Trappe 22757
*Geopora cooperi* var. *cooperi* (A): Trappe 22766
*Hydnotrya cubispora* (S, A): Trappe 22726, 22773
*Hydnotrya variiformis* (S): Trappe 22755
*Leucangium carthusianum* (S): Trappe 22769
*Leucangium* sp. nov. (S)[1]: Trappe 22763, 22764, 22767
*Tuber gardneri* (S, A): Trappe 22731
*Tuber gibbosum* (S): Trappe 22727, 22768
*Tuber monticola* (A): No collection retained
*Tuber oregonense* sp. nov. (A)[1]: Trappe 22753
*Tuber shearii* (A): Trappe 22729
*Tuber* sp. nov. (S)[1]: Trappe 22768

**Basidiomycota**

*Alpova diplophloeus* (A): Trappe 22761
*Gautieria monticola* (S): Trappe 22745
*Gymnomyces* sp. nov. (A)[1]: Trappe 22756
*Hymenogaster gilkeyae* (S): Trappe 22728, 22749
*Hymenogaster subalpinus* (A): Trappe 22750, 22752
*Hymenogaster sublilacinus* (S): Trappe 22751
*Hysterangium coriaceum* (S, A): No collections retained
*Hysterangium crassirhachis* (S): Trappe 22746
*Leucogaster citrinus* (S): No collection retained
*Leucophleps magnata* (S): Trappe 22754
*Melanogaster tuberiformis* (S): Trappe 22747
*Rhizopogon ater* (A)[1]: Trappe 22770
*Rhizopogon hawkerae* (A): Trappe 22771
*Rhizopogon parksii* (A): Trappe 22760, 22772
*Rhizopogon villosulus* (A): Trappe 22759
*Rhizopogon vinicolor* (S): Trappe 22762
*Truncocolumella citrina* (A): Trappe 22725

**Glomeromycota**

*Glomus macrocarpum* (S): Trappe 22758

**Zygomycota**

*Endogone flammicorona* (S): No specimen retained
*Endogone lactiflua* (S, A): Trappe 22748

[1]New species are given provisional names and will be described in separate papers.

TABLE 3. Sporocarp biomass and percent frequencies of hypogeous fungal genera in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands (3576-m$^2$ total sample area), Oregon Coast Range, 1996 and 1997.

| Genera | Number of Sporocarps | Dry weight (g) | % frequency of stands[1] | % frequency of plots[2] |
|---|---|---|---|---|
| *Alpova* | 24 | 6.8 | 3.8 | 42 |
| *Barssia* | 26 | 3.0 | 3.8 | 33 |
| *Elaphomyces* | 5 | 5.2 | 1.5 | 17 |
| *Endogone* | 16 | 1.0 | 6.8 | 58 |
| *Gautieria* | 12 | 7.7 | 2.3 | 17 |
| *Genea* | 15 | 0.9 | 1.5 | 17 |
| *Geopora* | 2 | 0.4 | 0.8 | 8 |
| *Glomus* | 3 | 0.1 | 2.3 | 25 |
| *Hydnotrya* | 21 | 1.1 | 6.8 | 42 |
| *Hymenogaster* | 10 | 1.9 | 5.3 | 25 |
| *Hysterangium* | 231 | 34.9 | 24.8 | 67 |
| *Leucangium* | 2 | 3.4 | 6.0 | 33 |
| *Leucophleps* | 29 | 0.1 | 0.8 | 8 |
| *Gymnomyces* | 1 | 0.7 | 0.8 | 8 |
| *Melanogaster* | 11 | 2.7 | 0.8 | 8 |
| *Rhizopogon* | 85 | 24.8 | 18.0 | 75 |
| *Truncocolumella* | 16 | 4.7 | 7.5 | 42 |
| *Tuber* | 54 | 6.8 | 18.8 | 92 |
| TOTAL | 566 | 106.2 | | |

[1]Percentage of total number of plots with truffles.
[2]Percentage of total number of stands.

TABLE 4. Sporocarp biomass by fungal genera (g/ha) from 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands during 3 seasons, Oregon Coast Range.

| Genera | Spring 1996 | Autumn 1996 | Spring 1997 | Total |
|---|---|---|---|---|
| *Alpova* | 0 | 689 | 0 | 689 |
| *Barssia* | 88 | 13 | 206 | 307 |
| *Elaphomyces* | 517 | 0 | 0 | 517 |
| *Endogone* | 86 | 1 | 13 | 100 |
| *Gautieria* | 209 | 0 | 560 | 769 |
| *Genea* | 0 | 0 | 93 | 93 |
| *Geopora* | 0 | 38 | 0 | 38 |
| *Glomus* | 0 | 0 | 11 | 11 |
| *Hydnotrya* | 88 | 10 | 12 | 110 |
| *Hymenogaster* | 107 | 67 | 15 | 189 |
| *Hysterangium* | 2523 | 234 | 743 | 3500 |
| *Leucangium* | 221 | 0 | 119 | 340 |
| *Leucophleps* | 0 | 0 | 14 | 14 |
| *Gymnomyces* | 0 | 60 | 0 | 60 |
| *Melanogaster* | 0 | 0 | 271 | 271 |
| *Rhizopogon* | 1231 | 1170 | 86 | 2487 |
| *Truncocolumella* | 0 | 470 | 0 | 470 |
| *Tuber* | 273 | 268 | 146 | 687 |
| TOTAL | 5343 | 3020 | 2289 | 10652 |

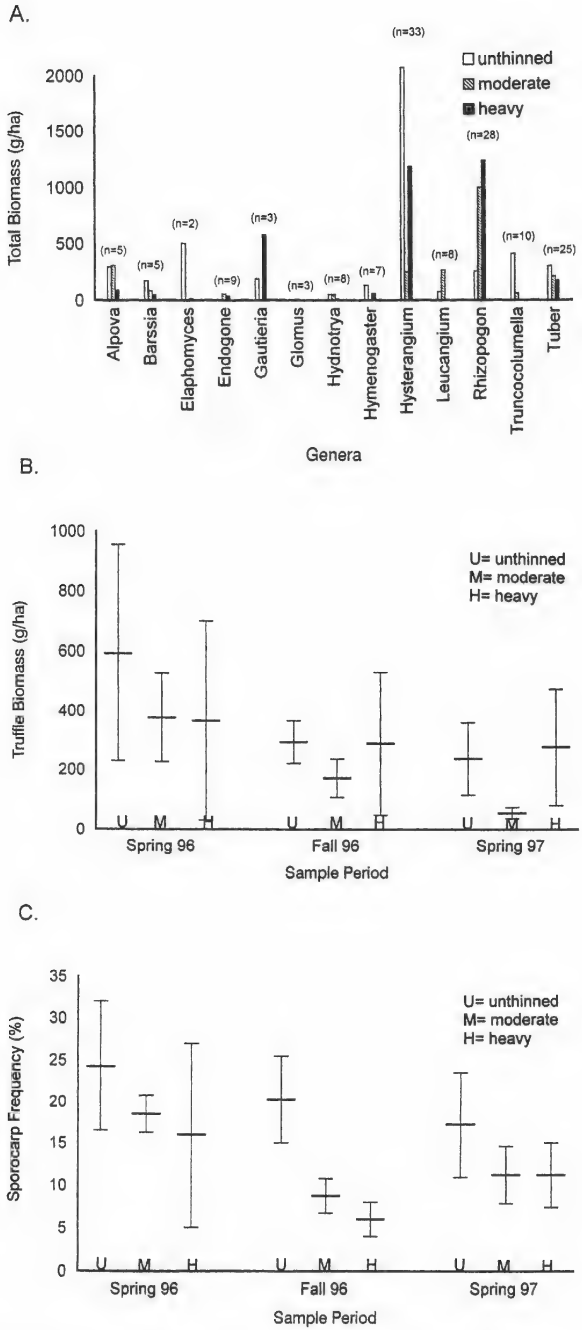


Figure 1. a) Total hypogeous sporocarp biomass of common genera by treatment; b) total sporocarp biomass and c) total frequency, in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997.

TABLE 5. Mean standing crop biomass (g/ha) of hypogeous fungal sporocarps by genus in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997. Means computed from mean of subsamples within each stand (n = 23-28).

| Genus | Unthinned | Moderate thinning | Heavy thinning | *P* value |
|---|---|---|---|---|
| *Endogone* | 1.3 ± 1.3 | 14.2 ± 7.8 | 9.5 ± 8.8 | 0.20[1] |
| *Hydnotrya* | 12.6 ± 7.6 | 12.3 ± 12.3 | 2.5 ± 2.5 | 0.44[1] |
| *Hysterangium* | 517.0 ± 408.9 | 62.6 ± 39.6 | 295.2 ± 271.8 | 0.46[1] |
| *Rhizopogon* | 64.4 ± 28.2 | 248.4 ± 137.7 | 308 ± 209.5 | 0.35[1] |
| *Tuber* | 75.5 ± 19.4 | 56.5 ± 26.2 | 43.6 ± 24.2 | 0.37[2] |
| Total biomass | 1124.9 ± 417.0 | 603.7 ± 177.6 | 934.5 ± 512.0 | 0.38 |

[1]Variable was $Log_{10}$ (X + 1) transformed.
[2]Variable was square-root transformed.

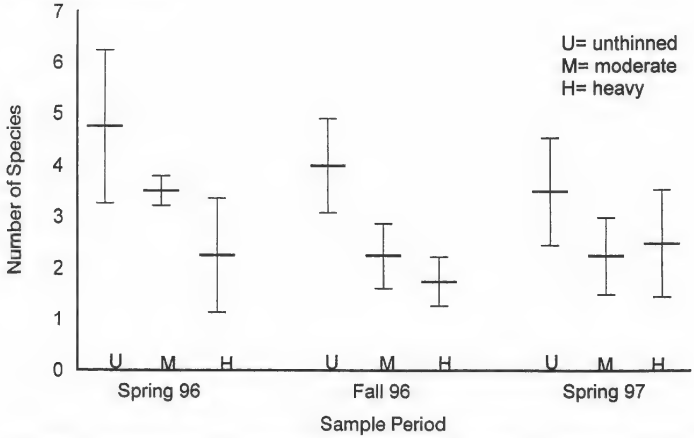


Figure 2. Mean number of hypogeous fungal species 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997.

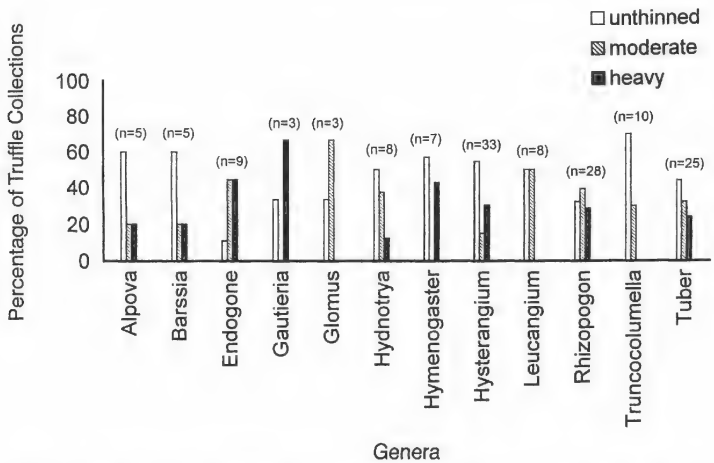


Figure 3. Percentage of hypogeous sporocarp collections of genera found in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997.

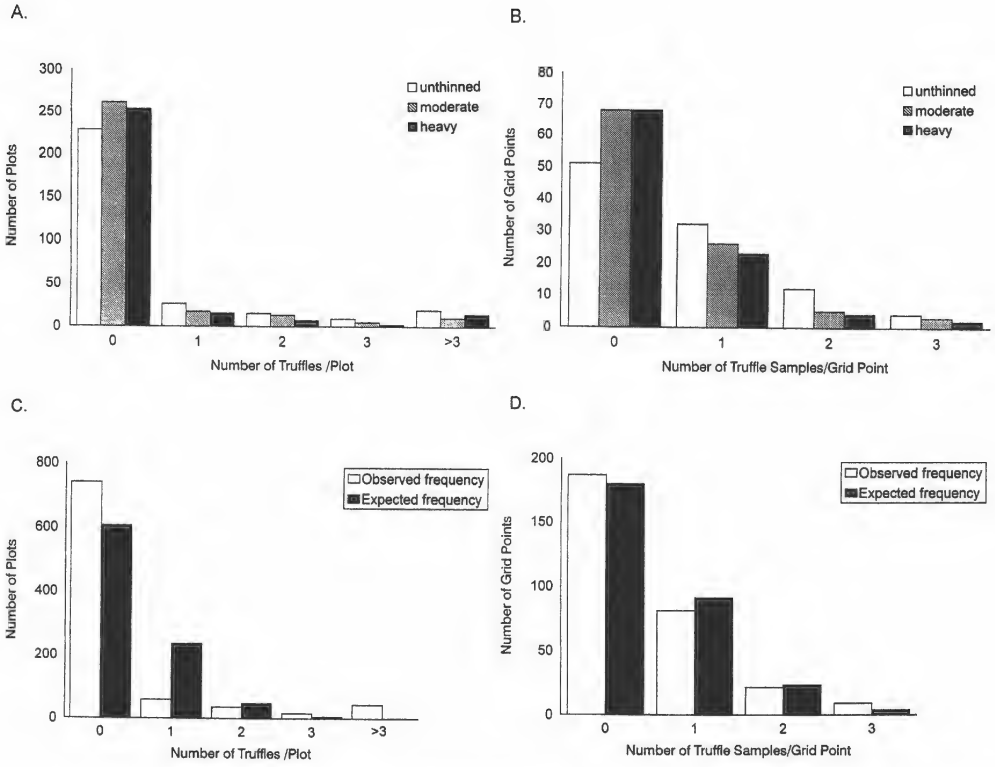


Figure 4. A) Frequency of hypogeous sporocarp plots with different numbers of sporcarps found per plot (n=894 total plots) in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997; B) frequency of grid points with different numbers of sporocarp samples per grid point (n=298 total grid points) by treatment; C) observed vs expected frequencies (based on Poisson distributions) of numbers of sporocarps found per plot (n=894 total plots); and D) observed vs expected frequencies (based on Poisson distributions) of numbers of sporocarp samples per grid point (n=298 total grid points) in Oregon Coast Range, 1996 and 1997.

tributed on the 4-$m^2$ plot scale for any of the nine season-by-treatment combinations ($P$<0.001 for each test) or when seasons and treatments were combined ($P$<0.001, Figure 4C). Sporocarps were randomly distributed among grid points for all study sites for all locations. When the data for locations were combined, however, the sporocarps were significantly clumped at grid points ($P$<0.05, Figure 4D).

### *Relationship between habitat variables and hypogeous sporocarp abundance*

Hypogeous sporocarp frequency was negatively associated with stump density (Y=0.59 - 0.0009X, $R^2$=0.42, $P$=0.02, Figure 5). Snag density ($X_1$), stump density ($X_2$), and large log density (≥50-cm diam, $X_3$) explained much of the variability in the regression model with sporocarp biomass (Y): $Y=487.4-7.21X_1-1.86X_2+3.66X_3$, $R^2$=0.64, $P$=0.04. Sporocarp biomass was negatively related to stump density (r=-0.40) and positively associated with large log density (r=0.38) in this model. Density of large snags (≥50-cm dbh, $X_1$), density of small logs (10-49-cm diam, $X_2$), density of large logs ($X_3$), and density of slash ($X_4$) explained a significant amount of the variability in the data set with sporocarp frequency (Y): $Y=0.03-0.13X_1-0.02X_2+0.17X_3-0.73X_4$, $R^2$=0.96, $P$=0.001. Sporocarp frequency was positively related to large log density (r=0.37) and negatively

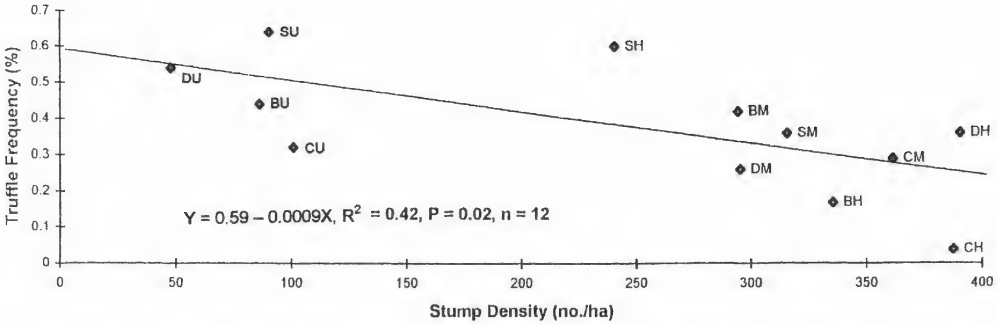


Figure 5. Relation between truffle percent frequency and stump density (no./ha), Oregon Coast Range, 1996 and 1997. Point labels designate stands (SU=Stimson unthinned, SM=Stimson moderate, SH=Stimson heavy, CU= C-line unthinned, CM= C-line moderate, CH= C-line heavy, DU=Deer Diamond unthinned, DM=Deer Diamond moderate, DH= Deer Diamond heavy, BU=Bensmith unthinned, BM=Bensmith moderate, BH=Bensmith heavy).

related to slash (r=-0.48) in this model. Large snags ($X_1$), stumps ($X_2$), and small logs ($X_3$) explained much of the variability in the regression model with *Hysterangium* standing crop biomass (Y): ($Y=1.23-0.47X_1-0.08X_2+0.04X_3$, $R^2=0.60$, $P=0.05$). *Hysterangium* biomass was negatively related to large snag density (r=-0.55) in this model. Large deciduous tree density (≥50-cm diam, $X_1$) small snag density (10-49-cm diam, $X_2$), large snag density ($X_3$), and slash density ($X_4$) explained much of the variability in the regression model with *Tuber* biomass (Y): ($Y=0.25+1.67X_1+0.05X_2-0.26X_3-0.003X_4$, $R^2=0.73$, $P=0.04$). *Tuber* standing crop biomass was positively related to large deciduous tree density (r=0.45).

## Discussion

The number of sporocarp-producing species (Table 2, Figure 2) and large proportion of sporocarp standing crop biomass produced by a relatively few of those species (Table 3) in our study agree with results of others in the Pacific Northwest, as reviewed by Carey et al. (2002). We hypothesized that sporocarp production and diversity would decrease with commercial thinning, because hypogeous fungi depend on their mycorrhizal host plants for photosynthates and their thalli tend to be concentrated in the upper mineral and organic soil, layers, which are disturbed during timber harvesting. Our data showed that commercial thinning reduced hypogeous sporocarp frequency and mean number of species fruiting at 2-3 yr after cutting (Figure 2). Colgan et al. (1999) drew similar conclusions from sampling within 3 yr since thinning. Photosynthetic potential is positively correlated with abundance of ectomycorrhizal fungal sporocarps in forests (Termorshuizen and Schaffers 1987). Our results may in part result from differences in photosynthetic potential of the host tree canopy between the thinned and unthinned stands together with loss of the fungus-supporting root systems of the cut trees, as also evidenced by the negative correlation of hypogeous sporocarp frequency and stump density (Figure 5).

No differences in sporocarp standing crop biomass could be detected in our data because of large variance. However, number of stumps was significantly greater on thinned than unthinned stands (Table 1) and sporocarp biomass and frequency were negatively related to number of stumps (Figure 5). The correlation analyses thus permit an inference that the larger the number of trees cut, the smaller the standing crop biomass. Colgan et al. (1999) drew similar conclusions, their study and ours both being 3 yr after thinning. In northern California, species composition of hypogeous sporocarps differed between thinned and unthinned stands 10 yr after thinning, but overall sporocarp standing crop biomass did not differ between treatments (Waters et al. 1994). The reduction of standing crop biomass with increasing number of trees cut in the short term thus may be mitigated over time. However, changes in the species of hypogeous fungal sporocarps can persist for a decade or more. We and Colgan et al. (1999) both showed the fruiting of fungal species differed between thinned and unthinned stands

within 3 yr after cutting (Table 5, Figure 1), and Waters et al. (1994) detected similar differences 10 yr after thinning. *Gautieria* and *Hysterangium* were more abundant in the unthinned stands than thinned both within 3 yr and after 10 yr of cutting (Waters et al. 1994, Colgan et al. 1999). This trend was not evident in our study, possibly because the climate and soils differed substantially from those of the other studies cited. The Coast Range of Oregon is characterized by relatively high rainfall and moderate temperatures that likely allow some species to better tolerate disturbance by thinning.

The higher sporocarp species richness in the unthinned than thinned treatment of our study (Figure 2) is noteworthy in light of the fungal species diversity common to the diet of small mammal mycophagists (Maser et al. 1978, 1985, Carey et al. 2002). This diversity may be a nutritional imperative for fungal specialists: Claridge et al. (1999) demonstrated by feeding trials that the northern flying squirrel (*Glaucomys sabrinus*) and California red-backed vole (*Clethrionomys californicus*) did not maintain their body weight on a diet solely of *Rhizopogon vinicolor.* Their chemical analyses of this fungus, which abounded both in our study and that of Colgan et al. (1999), showed a relatively low nutritional value to mammals. They suggested that a diet of diverse fungal species might be required to provide the needed array of dietary constituents. Northern flying squirrels supplement their diet with staminate catkins of conifers (Maser et al. 1985), mast of maples (Carey et al. (2002), and various other materials (Thysell et al. 1997). They are not highly mobile (Martin and Anthony 1999) but can readily visit a variety of habitats within their home range (Carey 2000). Small scale thinnings therefore may not seriously impinge on the amount or diversity of their food supply. Large scale thinnings, in contrast, could reduce quality of their habitat by decreasing the amounts or diversity of hypogeous sporocarps: we documented a positive relation between flying squirrel abundance and sporocarp biomass in a companion study to this one. The California red-backed vole, in contrast, an extreme mycophagist, typically ingests eight or more species of hypogeous fungi in a day (Maser et al. 1978) and has habitat requirements and behaviors that severely restrict its home range (Rosenburg et al. 1994, Maser 1998). Reducing fungal diversity in its habitat by thinning even on a relatively small scale could be seriously detrimental.

Sporocarp standing crop of nine hypogeous genera varied seasonally: total sporocarp standing crop was highest in spring 1996 and lowest in autumn 1997 (Table 4). Fungal species commonly fruit only in one particular season each year, but weather patterns within a season may also produce marked year-to-year variation (Fogel 1981, Eveling et al. 1990). Data must be collected over many years as done by Louma et al. (1991) to address seasonal relationships of any taxon adequately. Other species attributes may also come into play. For example, Johnson (1994) placed species into two groups based on sporocarp moisture content. Fleshy or succulent species with high moisture content fruited in response to rainfall or in cool months of the year, whereas species that form relatively dry sporocarps did not respond to rainfall. In our study only *Elaphomyces granulatus* would be categorized as having dry sporocarps, and its frequency was too low to evaluate effects of thinning.

Distributions of hypogeous sporocarps were clumped at the plot and grid station levels (Figure 4), and total sporocarp abundance was associated with abundance of CWD. Clearly, hypogeous sporocarps were not randomly distributed. Fogel (1976) and Hunt and Trappe (1987) also reported clumped distributions of hypogeous sporocarps. Hypogeous sporocarp production has been associated with CWD elsewhere (Amaranthus et al. 1994, Clarkson and Mills 1994) . This association likely results from the ability of decayed CWD to absorb and retain the moisture essential for hypogeous sporocarp production in dry months (Amaranthus et al. 1994). Clarkson and Mills (1994) suggested that the frequency of CWD use by some mycophagists would also increase the incidence of hypogeous sporocarps there, because that is where the spore-bearing feces are likely to be deposited. At the same time, the presence of the sporocarp food resource in and near decayed CWD would attract the animals. Most particularly, the occurrence of the fungal specializing California red-backed vole is strongly tied to CWD (Maser et al. 1978, Ure and Maser 1982, Maser 1998).

Commercial thinning in the Oregon Coast Range influenced hypogeous sporocarp production and species richness at 2-3 yr after cutting,

but the overall impact of thinning is difficult to assess because of seasonal and local fluctuations in hypogeous sporocarp populations. Because CWD was an important variable for predicting hypogeous sporocarp production, the retention of CWD in commercially thinned sites is likely important to sporocarp production of certain hypogeous species and to habitat maintenance for many small mammal mycophagists.

## Acknowledgements

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## Literature Cited

Amaranthus, M., J. M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24:2157-2165.

Brown, E. R., and A. B. Curtis. 1985. Introduction. Pages 1-15 *In* E. R. Brown (editor), Management of wildlife and fish habitats in forests of Western Oregon and Washington. USDA Forest Service Publication R6-F & WL-192-1985. Region 6, Portland, Oregon.

Carey, A. B. 2000. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. Pages 45-66 *In* R. L. Goldingay and J. S. Scheibe (editors), Biology of Gliding Mammals. Filander Verlag, Fürth, Germany.

Carey, A. B., W. Colgan III, J. M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science 72:148-157.

Claridge, A. W., J. M. Trappe, S. J. Cork, and D. L. Claridge. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor,* a common hypogeous fungus. Journal of Comparative Physiology B 169:172-178.

Clarkson, D. A., and L. S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Science 68:259-265.

Colgan III, W., A. B. Carey, J. M. Trappe, R. Molina, and D. Thysell. 1999. Diversity and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest. Canadian Journal of Forest Research 29:1259-1268.

Eveling, D. W., R. N. Wilson, E. S. Gillespie, and A. Bataille. 1990. Environmental effects on sporocarp counts over fourteen years in a forest area. Mycological Research 94:998-1002.

Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas Fir stand. Canadian Journal of Botany 54:1152-1162.

Fogel, R. 1981. Quantification of sporocarps produced by hypogeous fungi. Pages 553-568 *In* D. T. Wicklow and G. C. Carroll (editors), The Fungal Community, its Organization and Role in the Ecosystem. Marcel Dekker, New York.

Fogel, R., and J. M. Trappe. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science 52:1-31.

Hunt, G. A., and J. M. Trappe. 1987. Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. Canadian Journal of Botany 65:438-445.

Johnson C. 1994. Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: seasonal variation and annual production. Mycological Research 98:1173-1182.

Luoma, D. L., R. E. Frenkel, and J. M. Trappe. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. Mycologia 83:335-353.

Mallows, C. L. 1973. Some comments on Cp. Technometrics. 122:591-612.

Martin, K. J., and R. G. Anthony. 1999. Movements of northern flying squirrels in different-aged forest stands of western Oregon. Journal of Wildlife Management 63:291-297.

Maser, C. 1998. Mammals of the Pacific Northwest from the Coast to the High Cascades. Oregon State University Press, Corvallis, Oregon.

Maser, C., and J. M. Trappe (editors). 1984. The seen and unseen world of the fallen tree. USDA Forest Service General Technical Report PNW-164. Pacific Northwest Research Station, Portland, Oregon.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799-809.

Maser, Z., C. Maser, and J. M. Trappe 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084-1088.

Molina, R., H. Massicotte, and J. M. Trappe. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. Pages 106-112 *In* M. F. Allen (editor), Mycorrhizal Functioning-an Integrative Plant-Fungal Process. Chapman and Hall, New York.

Parks, H. E. 1919. Notes on California fungi. Mycologia 11:10-21.

Read, D. J., D. H. Lewis, A. H. Fitter, I. J. Alexander (editors). 1992. Mycorrhizas in Ecosystems. C.A.B. International, Wallingford, United Kingdom.

Rosenberg, D. K., K. A. Swindle, and R.G. Anthony. 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. Northwest Science 68:266-272.

Steel, R. D., and G. Torre. 1980. Principles and Procedures of Statistics: A Biometrical Approach. McGraw-Hill, New York.

Termorshuizen, A. J., and A. P. Schaffers. 1987. Occurrence of carpophores of ectomycorrhizal fungi in selected stands of *Pinus sylvestris* in the Netherlands in relation to stand vitality and air pollution. Plant and Soil 104:209 -217.

Thysell, D. R., L. J. Villa, and A. B. Carey. 1997. Observations of northern flying squirrel feeding behavior: use of non-truffle items. Northwestern Naturalist 78:87-92.

Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307-3315.

Vogt K. A., R. L. Edmonds, and C. C. Grier. 1981. Biomass and nutrient concentrations of sporocarps produced by mycorrhizal and decomposer fungi in *Abies amabilis* stands. Oecologia 50:170-175.

Waters, J. R., K. S. McKelvey, C. J. Zabel, and W. W. Oliver. 1994. The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi. Canadian Journal of Forestry Resources 24:1516-1522.

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# Environmental Contaminants and Nesting Behavior of Great Blue Herons from the Columbia and Willamette Rivers, Oregon and Washington

## Abstract

Reduced productivity and elevated contaminant concentrations have been documented in fish-eating birds, including bald eagles, from the Columbia River since 1984. To determine whether nest attendance was related to contaminant concentrations in eggs of fish-eating birds, we e"xamined breeding behavior of great blue herons at six colonies, in Oregon and Washington. We chose great blue herons as an indicator species for the effects of environmental contaminants on the guild of fish-eating birds because previous studies have demonstrated their utility. Patterns of attendance and nest visitation were significantly different among sites. The site with the highest concentrations of *p,p*'-DDE and total PCBs had significantly lower nest attendance relative to the reference site. Differences in nest attendance among colonies were inversely related to *p,p*'-DDE and PCB concentrations; however fledging and reproductive success in all colonies were similar to those reported for healthy populations. Differences in nest attendance and visitation among sites did not appear to be affecting nestling survival pre-fledging.

## Introduction

Altricial nestlings have three main requirements that must be met to insure their survival: protection, thermoregulation, and nutrition (Gill 1990). Protection of eggs and nestlings requires an adult to be present and defend the nest. Thermoregulation of eggs and chicks also requires nest attendance, and the adults must display proper incubation and brooding behaviors. Adults must also satisfy the daily energy requirements of their chicks by presenting a sufficient quantity and quality of food items, which requires a certain number of nest visits and proper feeding behaviors. Therefore, nest attendance is critical to successful reproduction. If a breeding pair does not meet these basic requirements, their reproductive success may be impaired.

In addition to direct mortality and teratogenicity, contaminants can have sublethal effects on the behavior of vertebrates. Organochlorine compounds (OC) have been implicated in abnormal breeding behavior in several bird species. Reduced nest attentiveness, nest defense, and hatch success in herring gulls (*Larus argentatus*), mallards (*Anas platyrhynchos*), merlins (*Falco columbarius richardsonii*), and ring doves (*Streptopelia risoria*) have been associated with elevated concentrations of DDE, PCBs, and other organochlorine pesticides (Keith 1966, Peakall and Peakall 1973, Fyfe et al. 1976, Fox et al. 1978, McArthur et al. 1983). Ring doves exposed to DDE also spent less time engaged in courtship activities and had delayed renesting and reduced clutches in renesting attempts (Haegele and Hudson 1973, 1977). Elevated levels of PCB, polychlorinated dibenzo-p-dioxins (PCDD) and polychlorinated dibenzo-furans (PCDF) were detected in eggs of Forster's terns (*Sterna forsteri*) and implicated in shorter incubation periods and lower reproductive success relative to an uncontaminated site (Kubiak et al. 1989).

Residues of OC and PCB have been documented in many species of piscivorous birds, mammals, and fish from the Columbia and Willamette rivers in Oregon and Washington (Blus et al. 1980, Henny et al. 1984, Fitzner et al. 1988, Schmitt et al. 1990, Parsons et al. 1991, Anthony et al. 1993, Henny et al. 1996). In the 1970s, PCB residues in mink (*Mustela vison*) and river otter (*Lutra canadensis*) from the Columbia River (Henny et al. 1981) exceeded concentrations known to cause total reproductive failure in laboratory studies (Platonow and Karstad 1973). Egg concentrations of DDE were associated with reduced productivity in bald eagles (*Haliaeetus leucocephalus*), and eggshell thinning in both nesting eagles and black-crowned night herons

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(*Nycticorax nyticorax*) along the Columbia River (Henny et al. 1984, Anthony et al. 1993). Residues of PCB and *p,p'*-DDE (DDE) were detected in all life stages of bald eagles during the 1980s (Anthony et al. 1993), which strongly implicated the Columbia River as a primary source of these contaminants.

Several contaminants including polychlorinated dibenzo-p-dioxins (PCDDs), DDE, and PCBs have been found at potentially hazardous concentrations in fish and wildlife from the Columbia and Willamette rivers. Studies conducted by the U.S. Environmental Protection Agency (1992) detected in some fish tetrachlorodibenzo-p-dioxin residues that exceeded guidelines for the protection of human health and resulted in the issuance of a total maximum daily load (TMDL) for dioxin in both rivers. Fish collected from the Portland Harbor of the Willamette River exhibited strongly induced cytochrome P450 1A1, which is indicative of exposure to TCDD (Curtis et al. 1993). PCDD concentrations in unhatched bald eagle and double-crested cormorant (*Phalacrocorax auritus*) eggs collected from the Columbia River Estuary (Anthony et al. 1993, U.S. Fish and Wildlife Service 1999) were similar to concentrations found in fish-eating birds from Michigan that had poor reproductive success (Kubiak et al. 1989). Since 1984, bald eagle productivity along the Columbia River has been reduced and has been associated with elevated concentrations of DDE and PCBs in eggs and carcasses (Anthony et al. 1993).

Although Anthony et al. (1993) associated contaminants with reduced bald eagle productivity along the Columbia River, they were not able to determine the factors responsible for the reduced productivity. Further evaluation of contaminant effects on piscivorous birds in the Columbia River systems was needed, but a replacement or surrogate species was needed in any additional studies to avoid additional impacts to bald eagles, which are listed under the Endangered Species Act as a threatened species. Previous studies demonstrated the utility of great blue herons (*Ardea herodias*) as an indicator species for contaminants in piscivorous birds (Elliot et al. 1989, Whitehead 1990), and have reported on productivity and nesting behaviors in areas not impacted by contaminants (Pratt 1970, McAloney 1973, Dowd and Flake 1984, Butler 1992). Therefore, we chose to use great blue herons as an indicator species for the effects of environmental contaminants on bald eagles and other piscivorous birds in the Columbia River system.

The purpose of this study was to determine whether environmental contaminants were elevated in great blue herons and whether contaminant concentrations were associated with adult behaviors potentially responsible for reduced productivity. We previously reported on the contaminant concentrations in eggs of great blue herons and on reproductive parameters likely to be directly impacted by elevated contaminant concentrations (Thomas and Anthony 1999). We now report on behavioral responses that may be influenced by environmental contaminants: patterns of nest attendance and nest visitation by adult great blue herons in northwest Oregon and Washington. We investigated whether patterns of parental nest attendance were different at contaminated sites versus an uncontaminated site, and whether among-site differences in parental nest attendance were related to contaminant concentrations in eggs. We focused on the presence of adults at the nest and the rate of nest visitation as measures of nest attendance and feeding rates, respectively.

## Study Area

Study sites were located in northwest Oregon and Washington (Figure 1). The colonies at Bachelor, Fisher, and Karlson islands were located on the lower Columbia River. Bachelor Island was 6.4 km upstream from a pulp and paper mill, and Fisher Island was 3.2 km downstream from the same mill. Karlson Island was in the Columbia River Estuary, 27.2 km downstream from the closest pulp and paper mill. The Molalla State Park and Ross Island colonies were located on the lower Willamette River. Molalla was 16 km upstream from the nearest pulp and paper mill; Ross Island was 22.4 km downstream. The reference site, Samish Island, was in Puget Sound, Washington, 60.8 km downstream from the nearest pulp and paper mill. We designated Samish as the reference site due to a previous study that detected low concentrations of most OC in heron eggs from that colony (Cobb et al. 1994). Average annual precipitation is 108 cm along the Columbia and Willamette rivers and 85 cm near Samish Island in the Puget Sound (Franklin and Dyrness 1988).

Karlson and Samish islands were in the transition zone between fresh and saltwater, and the

Figure 1. Great blue heron colony locations and distances from nearest pulp and paper mill (in km, + if colony is upstream from mill and – if colony is downstream from mill), 1994-1995.

remaining sites were on or near freshwater. With the exception of the Molalla site, all colonies were in tidal areas. With the exception of Karlson, all colonies were in black cottonwood trees (*Populus trichocarpa*). The Karlson colony was in Sitka spruce (*Picea sitchensis*).

## Methods

### Sampling

We used scan sampling to quantify nest attendance and breeding behaviors of nesting great blue herons from April through mid-July in 1994 and 1995. We controlled for any reaction to observer presence by initiating scans ~ 20 min after our arrival and entry into the blinds. We conducted scans every 10 min and recorded instantaneous observations (Altmann 1974) of adult behavior for every visible nest. Initially, ~ 30 nests in cottonwood colonies were observed during each scan. As the nesting season progressed, fewer nests were visible because of leaf cover. Consequently, we observed ~ 20 nests from weeks 5-9. Approximately 30 to 35 nests were visible at Karlson throughout the nesting season.

We also recorded information on weather and the presence of predators. Although other potential nest predators (such as red tail hawks [*Buteo jamaicensis*] and ravens [*Corvus corax*]) were observed at all colonies, the only predation attempts observed were on juvenile herons by bald eagles in Samish. Temperature and precipitation were recorded every hour or when conditions changed. Predator data included the time of appearance and departure, reactions of the herons to predators, and activity of the predator. We rated reactions of the herons as 0 (no reaction); 1 (alert behavior, including grunting); 2 (adults left nest but remained nearby); 3 (local flush—adults flew from nests only in the vicinity of the predator); 4 (colony flush). This scoring system allowed us to account for the variation in adult reaction resulting from

different levels of threat posed by different species. Activity categories for predators included flying through the colony, landing in the colony, or predation attempts.

Observation sessions lasted 4-5 hr. We used 40-60x spotting scopes, and observations were conducted from ground blinds or tree stands, depending on nest visibility at the site. Approximate distances between observers and nests ranged from 10-25 m. With the exception of Molalla, all study sites were tidally influenced. Because one of our sites was inaccessible at low tide, we visited all sites during high tide. Observation sessions were centered on high tide such that a 4 hr session would begin 2 hr before high tide. To determine when to initiate observations in Molalla, we extrapolated from the nearest location downstream on the Willamette River that was tidally influenced. All observations were diurnal and were conducted between 0615 and 2015 hr. We visited each colony approximately three times a month from April through July of 1994 and 1995 until the chicks were 9 wk old, for 74 -78 hr of observation at each site. The order in which colonies were visited was randomly selected each week.

### Statistical Analyses

We synchronized nesting chronologies at all sites by defining week 0 as the estimated peak of hatch. For the analysis of nest attendance, we grouped data into present or absent categories. Situations in which one or both adults were present at or near (within 1 m) the nest were included.

We developed a logistic regression model to test for among-site differences in parental nest attendance. We fit a main-effects model that included covariates identified as significant ($P \leq 0.05$) in a drop-of-deviance test (Ramsey and Schaffer 1997). Covariates included temperature, predator presence, time of day, week, and year. Precipitation was a significant explanatory variable for breeding behaviors but not for nest attendance. Because time (week) was a significant covariate, we then analyzed each week separately to determine when significant among-site differences were occurring. We used the Bayes Information Criteria to determine the best interaction model because it emphasizes parsimony of parameters by penalizing larger models (Ramsey and Schaffer 1997). Interactions between site and week, site and year, and temperature and week were tested. All odds ratios were calculated using Samish as the reference for comparison. We transformed the attendance odds ratios using the natural log to normalize the data, and used simple linear regression to test for relationships between odds ratios and contaminant concentrations.

We counted the number of landing calls by visit, adjusted the total for each site by colony size, and used a square-root transformation to normalize the distribution. Due to small degrees of freedom (six study sites), site comparisons were restricted to paired comparisons of reference versus non-reference sites. We calculated Wilks' lambda and used the Bartlett's approximation to derive $\chi^2$ (Mardia et al. 1979) to determine whether there was an overall difference in nest exchange rates between reference and non-reference sites. We developed multivariate models to determine whether the number of nest visits was related to year and site effects after accounting for weather and predator effects. We then developed separate multiple linear regressions for each week to examine when the counts were significantly different between reference and non-reference sites. We report significant results using $P = 0.05$.

## Results

### General Trends

During both 1994 and 1995, nesting chronology varied by ~2 wk within the six colonies studied. Herons in colonies at Bachelor, Fisher, Molalla, and Ross generally initiated incubation in mid-March. Estimated peak of hatch for these colonies was in mid-April. In contrast, colonies at Karlson and Samish generally initiated incubation in the end of March/beginning of April; estimated peak of hatch for these two colonies was in early May. The estimated peak of fledge followed a similar pattern, with juvenile herons from Bachelor, Fisher, Molalla, and Ross fledging in early to mid-June, while Karlson and Samish fledged the maximum number of young in late June to early July. The timing of incubation and peak of hatch was consistent between years, whereas the peak of fledge was earlier by at least one week in 1995 for all colonies except Samish.

During both 1994 and 1995, colonies at Bachelor, Fisher, Karlson, and Samish were adjacent to active bald eagle nests. We observed bald eagle intrusions in the Fisher, Karlson, and Samish colo-

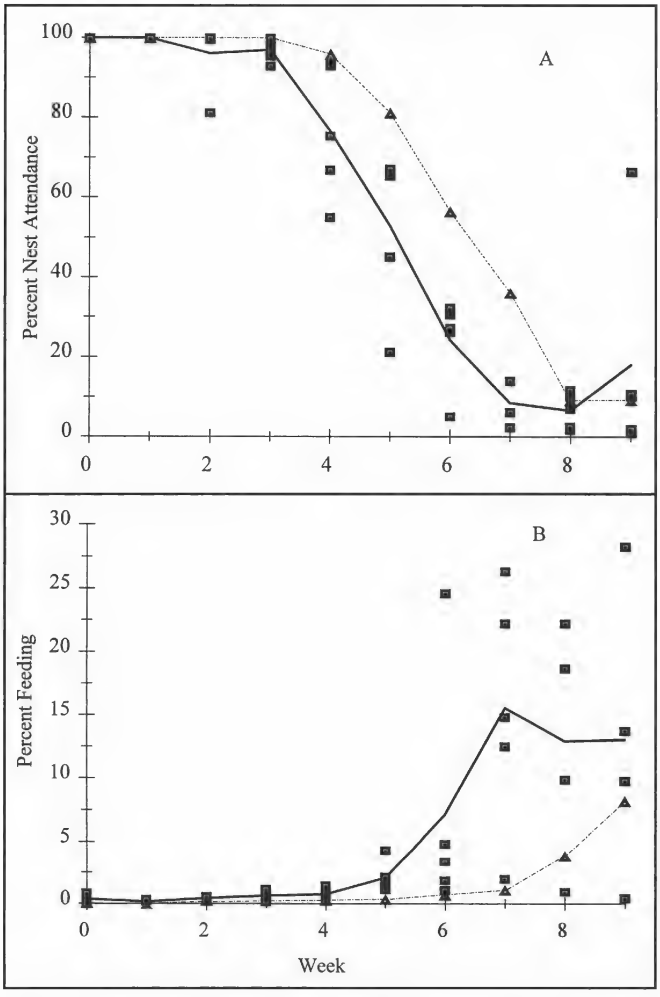


Figure 2. Percent of adult herons in attendance (A) and feeding (B) in six western Oregon and Washington colonies each week, 1994-1995. Triangles and broken line represent reference site, squares and solid line represent non-reference sites.

nies. We observed one successful predation event by a bald eagle in Samish, in which the bald eagle flew out of sight with a 3-4 wk-old heron while the adults were not attending the nest.

The rate of nest visits changed greatly with time over the breeding season. The percentage of adults present at a nest followed a sigmoid curve (Figure 2A). One or both adults were continuously present at most nests during weeks 0-3, then adult attendance declined rapidly, and few adults were present at their nests during the last 2 wk of the nesting period. Throughout the nesting cycle, adults at Samish were present at their nests more than at other sites. The percentage of adults feeding chicks increased after week 4 (Figure 2B).

## Contaminants

Contaminant data from 1994 and 1995 were not significantly different for *p,p'*-DDE, total PCBs, or 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD),

TABLE 1. Organochlorine concentrations (fresh wet weight) in great blue heron eggs (N=10) from the Columbia and Willamette rivers and Puget Sound, 1994-95. Data are adapted from Thomas and Anthony (1999). Results are geometric means and (95% confidence intervals). Results for DDE and PCB are reported in ng/g, TCDD results are reported in pg/g. Means with identical superscripts are not significantly different.

| | Bachelor | Fisher | Karlson | Molalla | Ross | Samish |
|---|---|---|---|---|---|---|
| p,p'-DDE | 331[a] | 393[a] | 852[a] | 520[a] | 1432[b] | 121[a] |
| | (190-575) | (196-788) | (657-1105) | (269-1005) | (554-3703) | (81-182) |
| Total | 480[a] | 744[ab] | 1574[ab] | 474[a] | 2842[b] | 292[a] |
| | (308-747) | (403-1377) | (1158-2132) | (310-726) | (1120-7214) | (194-438) |
| 2,3,7,8- | 2.57 | 2.94 | 7.42 | 3.10 | 5.08 | 2.44 |
| TCDD | (1.68-3.93) | (1.52-5.69) | (5.12-10.76) | (2.50-3.85) | (2.31-11.19) | (1.42-4.20) |

so data from the 2 years were pooled. Significant among-site differences were present in concentrations of *p,p'*-DDE ($P < 0.001$), total PCBs ($P = 0.01$) and TCDD ($P = 0.03$). Eggs from Ross Island contained the highest concentrations of both DDE and total PCBs; eggs from Karlson Island contained the most TCDD (Table 1).

## Nest Attendance

Location was a significant explanatory variable ($P < 0.005$) for differences in nest attendance after accounting for differences in year, week, time of day, temperature, and presence of predators as covariates. Week ($P < 0.001$), temperature ($P < 0.001$), and time of day ($P < 0.001$) were also significant explanatory variables; the remaining variables were included in the model to account for known sources of variability.

The overall odds ratio (the likelihood of an event occurring) of at least one adult heron being present at the nest was significantly ($P < 0.05$) lower for all non-reference sites compared to Samish (Table 2). Patterns of adult nest attendance were most similar between Fisher and Samish. The odds ratio for adult presence was lowest for Ross and was 0.05 times the odds of adults being present at Samish. The log of odds ratios for adult nest attendance were negatively correlated with DDE ($r = -0.78$, $P = 0.01$) and PCB ($r = -0.64$, $P = 0.04$) concentrations (Figures 3 and 4), but not with TCDD concentrations. PCB and DDE concentrations in eggs were collinear ($P = 0.001$).

There were significant interactions between the year, week, and site effects on the probability of nest attendance by adult herons (Table 2). Compared to Samish, the odds ratio for at least one adult being present at its nest was greater in 1994 for the Fisher and Karlson colonies. For Bachelor, Molalla, and Ross colonies, the odds of adults being present were greater in 1995 relative to Samish. Significant interactions were detected between site and week relative to Samish. At Bachelor, Fisher, Molalla, and Ross, the odds ratios for adult nest attendance increased with successive weeks, compared to Samish. With the exception of Karlson, adults at non-reference sites appeared to be present later in the season. The odds of Karlson adults being present at the nest relative to Samish decreased with successive weeks. The temperature-by-week interaction was not significant for any model.

TABLE 2. Odds ratios and (95% confidence intervals) for main effects and interaction terms for great blue heron nesting behaviors (N = 2084), Columbia and Willamette rivers, 1994-1995. All odds ratios were calculated relative to Samish, the reference site. All odds ratios are significant at $P \leq 0.05$.

| Model | Bachelor | Fisher | Karlson | Molalla | Ross |
|---|---|---|---|---|---|
| Main effect | 0.38 | 0.51 | 0.40 | 0.25 | 0.05 |
| | (0.34-0.41) | (0.46-0.56) | (0.37-0.44) | (0.22-0.27) | (0.04-0.06) |
| Interactions | | | | | |
| Site x Week | 1.32 | 1.23 | 0.83 | 1.30 | 1.48 |
| | (1.24-1.41) | (1.15-1.31) | (0.77-0.90) | (1.22-1.39) | 1.37-1.60) |
| Site x Year | 0.55 | 2.62 | 1.77 | 0.78 | 0.16 |
| | (0.45-0.67) | (2.16-3.18) | (1.44-2.17) | (0.64-0.96) | (0.13-0.20) |

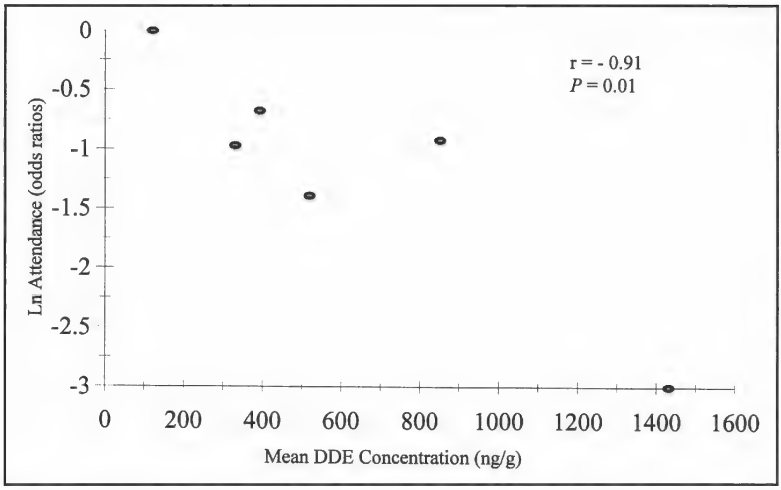


Figure 3. Negative correlation between natural log-transformed odds ratios for adult nest attendance and DDE concentrations (site means in ng/g wet weight) in great blue heron eggs from the Columbia and Willamette rivers and Puget Sound, 1994-1995.

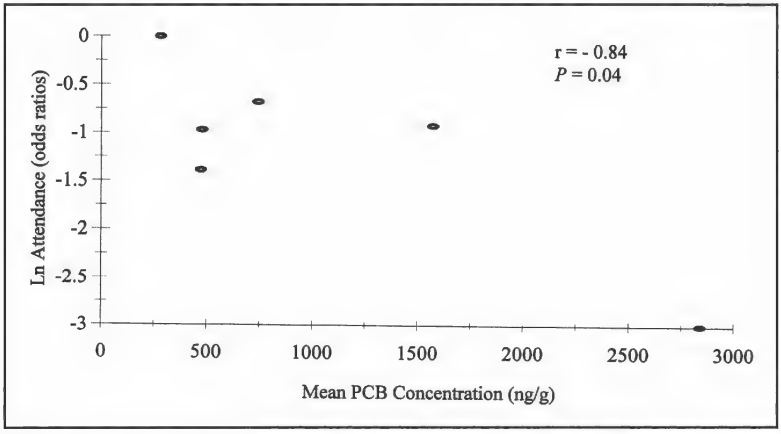


Figure 4. Negative correlation between natural log-transformed odds ratios for adult nest attendance and PCB concentrations (site means in ng/g wet weight) in great blue heron eggs from the Columbia and Willamette rivers and Puget Sound, 1994-1995.

### Nest Visits

The rate of nest visits peaked at week 2 and gradually declined to week 9 (Figure 5). After accounting for the effects of temperature, precipitation, predator presence, week, and year as covariates, rates of nest visitation at Samish differed significantly from all other sites ($P < 0.001$). Rates of nest visits at Samish were greater relative to non-reference sites during weeks 0-2. No difference was detected in visitation rates between Samish and non-reference sites during weeks 3-9.

## Discussion

Patterns of parental nest attendance and nest visitation were different among sites. Nest attendance was inversely related to DDE and PCB concentrations in eggs. However, the reproductive output of all six colonies was similar to that reported

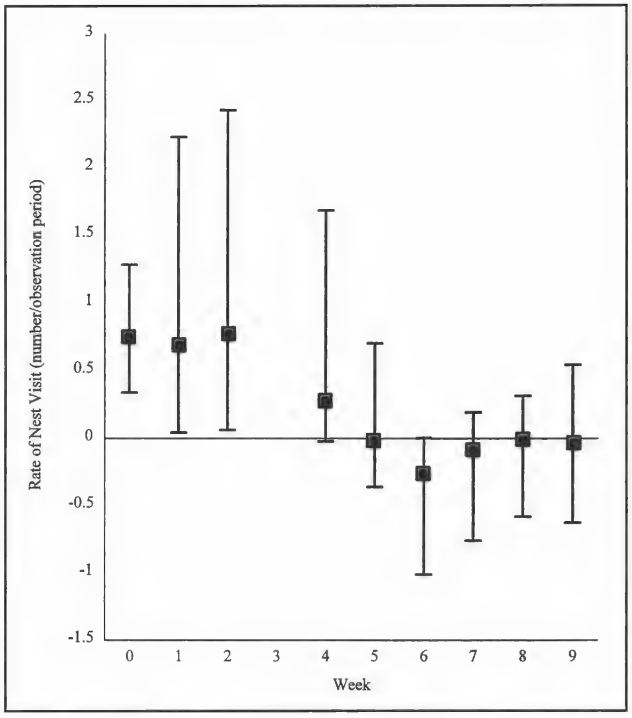


Figure 5. Parameter estimates and 95% confidence intervals for rate of nest visitation over time at reference site relative to non-reference sites for six great blue heron colonies, Columbia and Willamette rivers and Puget Sound, 1994-1995. Total number of nest visits were summed by observation period and adjusted for colony size.

for healthy populations of great blue herons (McAloney 1973, Blus et al. 1980, Dowd and Flake 1984, Fitzner et al. 1988). The differences we observed in nest attendance and rate of nest visits did not affect hatching success or nestling survival up to fledging.

The nest attendance patterns that we observed were similar to other studies of great blue herons in California (Pratt 1970) and South Dakota (Dowd and Flake 1984). In all three studies, adults displayed nearly constant nest attendance during weeks 2-3 posthatch, with attentiveness dropping sharply after week 4. McAloney (1973) reported nearly continuous brooding of chicks for the first 2 wk posthatch.

The percentage of adults observed feeding juveniles while at their nests increased during the last third of the nesting cycle. Because feeding sessions were brief and were infrequently observed, the rate of nest visitation provides a better indication of feeding frequencies at each site. The feeding frequencies presented here are slight overestimates because every nest visit did not result in feeding of the young.

The pattern that we observed in nest visits agreed with previous studies, which suggested that younger chicks are fed more often (Pratt 1970, Dowd and Flake 1984). The highest rate of nest visitation in this study occurred during week 2 posthatch, which was 2 wk earlier than peaks reported for herons nesting in British Columbia (Butler 1992) and South Dakota (Dowd and Flake 1984). Energy demands of captive great blue herons are greatest between weeks 4-6 (Butler 1993), which has important implications for chicks in our study areas. If the feeding pattern of the adults

does not match the growth pattern of the chicks, chicks may grow more slowly or have insufficient lipid reserves at fledging. Prey capture rates of juvenile herons are roughly half that of adults during the 2 mo following fledging (Quinney and Smith 1980), so that lipid reserves are crucial for survival during this period.

There were large differences in bald eagle presence among the sites. During 1994-95, active bald eagle nests were adjacent to the heron colonies on Bachelor, Fisher, Karlson, and Samish islands. Eagles were observed in the Samish colony during 14 out of 18 visits, for a total of 8.4% (370 of 4,424 min) of our observation time. Bald eagles were observed during 2 out of 18 visits for a total of 0.4% (18 out of 4,568 min) of our observation time at Fisher, and during 3 out of 18 visits (4 out of 4,570 min or 0.09%) to Karlson. Eagle intrusions were not observed at the Bachelor, Molalla, or Ross Island colonies. Adult great blue herons reacted strongly to the presence of bald eagles with alarm calls and increased vigilance behaviors. However, increased vigilance of Samish adults from frequent presence of bald eagles was not sufficient to explain among-site differences in nesting behaviors. Behavioral differences among sites were still significant after accounting for the presence of predators.

In previous studies, alterations in patterns of nest attendance, feeding, and incubation have most commonly been associated with environmental contaminants. In laboratory studies using ring doves (*Streptopelia risoria*), significant alterations in the amount of time involved in courtship activity were observed in birds fed elevated concentrations of DDE relative to control birds (Haegele and Hudson 1973, 1977). Altered courtship behavior, reduced nest attendance, and increased length of breeding cycle have also been observed in ring doves dosed with combinations of DDE and PCB (McArthur et al. 1983). In high-dose doves, effects also included prolonged incubation period, reduced brooding and feeding, and decreased fledge success.

Similar trends have been observed in field studies. Altered incubation behavior and altered minimum flushing distance were observed in herring gulls (*Laurus argentatus*) exposed to elevated levels of DDT and DDE (Keith 1966, Fox et al. 1978). Increased length of incubation and increased nest abandonment were observed in Forster's terns exposed to OC compounds including dioxins, furans, and PCB (Kubiak et al. 1989). Reduced nest defense in prairie falcons (*Falco mexicanus*) and merlins was associated with elevated concentrations of DDE and possibly PCB (Fyfe et al. 1976).

The TCDD and PCB concentrations observed during this study (2.4 to 7.4 pg/g, and 0.29 to 2.8 pg/g) were lower than those observed in Kubiak et al. (1989), and may be below the threshold that adversely affects survival through altered adult behavior. DDE concentrations (0.12 to1.4 pg/g) in our study, however, were similar to levels observed to cause abnormal nesting behavior in herring gulls and prairie falcons (Keith 1966, Fyfe et al. 1976).

Differences in nest attendance among sites were correlated with DDE and PCB concentrations in eggs. Eggs from Ross Island had the highest concentrations of DDE and PCB; these adults spent the least amount of time at their nests. In contrast, eggs from Samish contained the lowest concentrations of all three organochlorine contaminants, and adults spent the greatest amount of time at their nests. Adults at Samish also maintained higher rates of nest visitation, relative to all other sites, during the first 4 wk after the peak of hatch. These results suggest that contaminants affected nest attendance and prey delivery of herons in this study.

Although we suggest that contaminants had an effect on breeding behavior of great blue herons, other factors could have been responsible for differences in behavior among the colonies. Prey size and availability could have differed among the colonies and may be responsible for the among-site differences we observed in adult nest attendance. Prey may be more available at Samish relative to the rest of the sites. Herons typically feed in water less than 60 cm deep (Butler 1992), and Samish Island was adjacent to extensive eelgrass mudflats that may provide optimal foraging habitat at low tide. Typical feeding areas of herons on the Columbia and Willamette rivers include backwater sloughs that are frequently steep-sided, thus providing smaller areas of suitable habitat nearby. The distance to foraging areas was short and similar for all colonies.

Herons may also be selecting prey of different sizes at Samish compared to the non-reference sites. Herons at Samish appeared to make a

greater number of short trips to foraging areas, resulting in a higher rate of nest visitation, and allowing greater nest attendance relative to other sites. In contrast, herons on the Columbia and Willamette rivers may make fewer, longer trips to foraging areas, resulting in lower rates of nest visitation. According to the optimal foraging theory (Schoener 1969), predators that pursue their prey over greater distances should take larger prey to maximize net energy intake. For a unit increase in the distance between predator and prey, the change in handling time (amount of energy spent capturing prey per unit energy derived from prey per unit time) is larger for smaller prey. Consequently, for larger foraging distances, the minimum prey size must be larger for predators to maintain a positive energy balance. Only large prey should be taken at great distances, but the largest prey taken at a given distance may be smaller than the largest taken at smaller distances. Thus, the chicks at Samish may be fed more frequently with prey items of a smaller average size relative to non-reference sites. Chicks at the non-reference sites may be fed prey items of a larger average size less frequently. Although the prey we collected for contaminant analyses did appear to be smaller than prey collected from non-reference sites, we did not collect data on individual prey size and are unable to test that aspect of our theory. These factors should be considered when interpreting our results, and in future studies.

Although colonies exhibited healthy rates of hatch, fledge, and reproductive success, patterns of adult nest attendance were different among sites. The differences we observed in nesting behavior and residue levels did not affect survival of juvenile herons up to fledging. However, additional study is needed to determine the effect of current contaminant loads on juvenile fledging success.

## Acknowledgements

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## Literature Cited

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227-267.

Anthony, R. G., M. G. Garrett, and C. Schuler. 1993. Environmental contaminants in bald eagles in the Columbia River Estuary. Journal of Wildlife Management 57:10-19.

Blus, L. J., C. J. Henny, and T. E. Kaiser. 1980. Pollution ecology of breeding great blue herons in the Columbia Basin, Oregon and Washington. Murrelet 61:63-71.

Butler, R. W. 1992. Great Blue Heron. Pages 1-20 *In* A. Poole, P. Stettenheim and F. Gill (editors), The Birds of North America, no. 25. Academy of Natural Sciences; Washington, D.C.

Butler, R. W. 1993. Time of breeding in relation to food availability of female great blue herons (*Ardea herodias*). Auk 110:693-701.

Cobb, G. P., D. M. Norman, and R. J. Kendall. 1994. Organochlorine contaminant assessment in great blue herons using traditional and nonlethal monitoring techniques. Environmental Pollution 83:299-309.

Curtis, L. R., H. M. Carpenter, R.M. Donohoe, D.E. Williams, O.R. Hedstrom, M.L. Deinzer, M.A. Bellstein, E. Foster, and R. Gates. 1993. Sensitivity of cytochrome P450-1A1 induction in fish as a biomarker for distribution of TCDD and TCDF in the Willamette River, Oregon. Environmental Science and Technology 27:2149-2157.

Dowd, E. M., and L. D. Flake. 1984. Great blue heron nesting biology on the James River in South Dakota. Prairie Naturalist 16:159-166.

Elliot, J. E., R. W. Butler, R. J. Norstrom, and P. E. Whitehead. 1989. Environmental contaminants and reproductive success of great blue herons *Ardea herodias* in British Columbia, 1986-87. Environmental Pollution 59:91-114.

Fitzner, R. E., L. J. Blus, C.J. Henny, and D.W. Carlile. 1988. Organochlorine residues in great blue herons in the northwestern United States. Colonial Waterbirds 11:293-300.

Fox, G. A., A. P. Gilman, D. B. Peakall, and F. W. Anderka. 1978. Behavioral abnormalities of nesting Lake Ontario herring gulls. Journal of Wildlife Management 42:477-483.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Fyfe, R. W., R. W. Risebrough, and W. Walker II. 1976. Pollutant effects on the reproduction of the prairie falcons and merlins of the Canadian prairies. Canadian Field-Naturalist 90:346-355.

Gill, F. B. 1990. Ornithology. Freeman, New York.

Haegele, M. A., and R. H. Hudson. 1973. DDE effects on reproduction of ring doves. Environmental Pollution 4: 53-57.

Haegele, M. A., and R. H. Hudson. 1977. Reduction of courtship behavior induced by DDE in male ringed turtle doves. Wilson Bulletin 89:593-601.

Henny, C. J., L. J. Blus, S. V. Gregory, and C. J. Stafford. 1981. Pages 1763-1780 *In* J. A. Chapman and D. Pursely (editors), PCBs and organochlorine pesticides in wild mink and river otters from Oregon. Worldwide Furbearer Conference Proceedings, Aug 3-11, 1980. Frostburg, Maryland.

Henny, C. J., L. J. Blus, A. J. Krynitsky, and C. M. Bunck. 1984. Current impact of DDE on black-crowned night herons in the intermountain west. Journal of Wildlife Management 48:1-13.

Henny, C.J., R.A. Grove, and O.R. Hedstrom. 1996. A field evaluation of mink and river otter on the Lower Columbia River and the influence of environmental contaminants. Final Report for the Lower Columbia River Bi-State Water Quality Program. National Biological Service, Northwest Research Station, Corvallis, Oregon.

Keith, J. A. 1966. Reproduction in a population of herring gulls (*Larus argentatus*) contaminated by DDT. Journal of Applied Ecology 3 (Supplement): 57-70.

Kubiak, T. J., H. J. Harris, L. M. Smith, T. R. Smith, T. R. Schwartz, D. L. Stalling, J. A. Trick, L. Sileo, D. E. Docherty, and T. C. Erdman. 1989. Microcontaminants and reproductive impairment of the Forster's tern on Green Bay, Lake Michigan—1983. Archives of Environmental Contaminants and Toxicology 18:706-727.

Mardia, K. V., J. T. Kent, and J. M. Bibby. 1979. Multivariate Analysis. Academic Press, New York.

McAloney, K. 1973. The breeding biology of the great blue heron on Tobacco Island, Nova Scotia. Canadian Field-Naturalist 87:137-140.

McArthur, M. B., G. A. Fox, D. B. Peakall, and B. R. Philogene. 1983. Ecological significance of behavioral and hormonal abnormalities in breeding ring doves fed an organochlorine chemical mixture. Archives of Environmental Contaminants and Toxicology 12:343-353.

Parsons, A. H., S. L. Huntley, E. S. Ebert, E. R. Algeo, and R. E. Keenan. 1991. Risk assessment for dioxin in Columbia River fish. Chemosphere 23:1709-1717.

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Peakall, D. B., and M. L. Peakall. 1973. Effect of polychlorinated biphenyl on the reproduction of artificially and naturally incubated dove eggs. Journal of Applied Ecology 10:863-868.

Platonow, N.S., and L.H. Karstad. 1973. Dietary effects of polychlorinated biphenyls on mink. Canadian Journal of Comparative Medicine 37:376-398.

Pratt, H. M. 1970. Breeding biology of great blue herons and common egrets in central California. Condor 72:407-416.

Quinney, T. E., and P. C. Smith. 1980. Comparative foraging behavior and efficiency of adult and juvenile great blue herons. Canadian Journal of Zoology 58:168-1173.

Ramsey, F. L., and D. W. Schaffer. 1997. Statistical Sleuth: A Course in Methods of Data Analysis. Duxbury Press, Belmont, California.

Schmitt, C. J., J. L. Zajicek, J. L, and P.H. Peterman. 1990. National contaminant biomonitoring program: residue of organochlorine chemicals in freshwater fish, 1976-1984. Archives of Environmental Contaminants and Toxicology 19:748-781.

Schoener, T. W. 1969. Models of optimal size for solitary predators. American Naturalist 103:277-313.

Thomas, C. M., and R. G. Anthony. 1999. Environmental contaminants in great blue herons (*Ardea herodias*) from the lower Columbia and Willamette Rivers, Oregon and Washington, USA. Environmental Toxicology and Chemistry 18:2804-2816.

U.S. Environmental Protection Agency. 1992. National study of chemical residues in fish. Office of Science and Technology, Washington, D.C. 2 Volumes. (EPA 823-R-92-008a and EPA 823-R-92-008b).

U.S. Fish and Wildlife Service. 1999. Organochlorine contaminants in double-crested cormorants from Lewis and Clark National Wildlife Refuge in the Columbia River Estuary. Unpublished report on file at Oregon Fish and Wildlife Office, Portland, Oregon.

Whitehead, P. E. 1990. Toxic chemicals in great blue heron (*Ardea herodias*) eggs in the Strait of Georgia. Pages 177-183 *In* K. Vermeer and R.W. Butler (editors), The status and ecology of marine and shoreline birds in the Strait of Georgia, B.C. Canadian Wildlife Service, Ottawa.

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# Northern Goshawk Breeding Ecology and Nestling Growth in Mixed Coniferous Forests of West-Central Idaho

## Abstract

This study documented the nesting chronology, productivity, and nestling growth of northern goshawks in west-central Idaho in 1998 and 1999. Egg laying began in late April, and fledging occurred in mid-July. Goshawks used >35% of historical territories and eleven new territories were discovered. Of 46 occupied territories, 80% were successful, fledging one to four young. Productivity averaged 2.1 fledglings/successful nest in 1998 and 2.0 fledglings/successful nest in 1999. Failure rates were similar between years; 17% of occupied territories failed in 1998 and 21% failed in 1999. We also measured nestling growth, a variable not previously reported for goshawks in any northwestern studies. Time for nestlings to grow from 10 to 90% of their fledging mass ranged from 16 to 35 days and their growth-rate constants, $k$, ranged from 0.13 to 0.27. Nestling growth rates were similar within nests, but varied among nests. The fastest mean growth at a nest was 17 days to reach 90% of fledging mass, while the slowest mean growth was 33 days to reach 90% of fledging mass. Variability in growth among nests suggested there were differences in energy intake by nestlings, potentially due to adult condition or habitat quality. Nestling growth may be a valuable indicator of habitat quality and adult breeding condition during the nestling stage. In contrast, productivity (as defined in this study) can be viewed as a more encompassing expression of habitat quality including quality of the adult winter range and breeding habitat.

## Introduction

Northern goshawks (*Accipiter gentilis*) are found throughout forested portions of the intermountain west (Squires and Reynolds 1997) where they are designated as a Sensitive Species by the USDA Forest Service (USFS) (USDA Forest Service 1990, Squires and Reynolds 1997) and as a Species of Special Concern by the Idaho Department of Fish and Game (Beals and Harris 1996). Part of agency requirements under these designations include assessing potential impacts of habitat alteration actions on goshawks (Squires and Reynolds 1997). In Idaho, the presence of breeding goshawks can necessitate the creation of buffer zones around nests or the delay of land management activities until late summer after juvenile goshawks have fledged (Beals and Harris 1996; USDA Forest Service 2000a, 2000b). Basic knowledge of goshawk breeding was needed in west-central Idaho. Specifically, the objectives of our study were to: document egg laying, hatching, and fledging chronology, document the levels and consistency of territory occupancy and productivity, and document nestling growth rates. We hypothesized that territory occupancy, productivity, and nestling growth would differ among nest areas due to differences in habitat and adult breeding condition.

Nest chronology is not well documented in west-central Idaho, yet it is important to consider when scheduling activities potentially disturbing to breeding goshawks (Fyfe and Olendorff 1976, Fuller and Mosher 1987). Nesting chronology can be influenced by a number of factors including elevation, habitat quality, prey abundance and availability, spring weather, and disturbance (Newton 1979, Squires and Reynolds 1997). Raptors are most sensitive to disturbance during the prelaying period (Fyfe and Olendorff 1976).

Nest occupancy and productivity can be affected by habitat alteration ( e.g., Woodbridge and Detrich 1994, Widén 1997, Crocker-Bedford 1998), human disturbance (Boal and Mannan 1994), age and condition of breeders (Reynolds et al. 1994, Squires and Reynolds 1997), and interspecific competition (Crocker-Bedford 1990,

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Patla 1997). At scales larger than the nest area (e.g., breeding territory, subpopulation distribution) habitat components are often more variable. For example, prey abundance (Doyle and Smith 1994, Squires and Reynolds 1997), habitat structure relating to prey accessibility (Widén, 1989, Beier and Drennan 1997), weather (Kostrzewa and Kostrzewa 1991, Younk and Bechard 1994, Patla 1997, Penteriani 1997), and nestling predation (Boal and Mannan 1994) can regionally affect productivity. Boal and Mannan (1994) reported great horned owl (*Bubo virginianus*) predation as the single greatest factor contributing to goshawk nestling mortality in their Arizona study. Productivity estimates for goshawk breeding pairs in the northwestern United States range from 0.3 – 2.2 young per occupied nest (Bull and Hohmann 1994, DeStefano et al. 1994, Woodbridge and Detrich 1994, Patla 1997, Finn 2000). There is no published productivity information for goshawks nesting in west-central Idaho.

Nestling growth has not been described for goshawks in the United States with the exception of an admittedly incomplete growth curve (Schnell 1958). Nestling growth can be an important measure of adult fitness and habitat quality (Ross 1980, Quinney et al. 1986, Bortolotti 1989). In any given year, nestling growth and the number of offspring produced is limited by the ability of adult goshawks to obtain food (Ricklefs 1969). Studies on bald eagles (*Haliaeetus leucocephalus*) and Swainson's hawks (*Buteo swainsoni*) demonstrated the importance of food abundance and availability to nestling growth and survival (Bechard 1983, Bortolotti 1989). Bortolotti (1989) and Bechard (1983) imply that habitat conditions or adult foraging abilities in individual territories were more important determinants of nestling growth than individual nestling behavior, nestling competition, or morphology.

A gradient of increasing growth rates from larger to smaller species follows Ricklefs' (1967, 1973) hypothesis that variation in growth rates among species can be explained by adult body size. Slower growth rates exist for larger species such as golden eagle (*Aquila chrysaetos*) and great horned owl and faster growth rates exist for smaller species such as Cooper's hawk (*Accipiter cooperi*) and American kestrel (*Falco sparverius*) (Ricklefs 1973). Ricklefs' hypothesis would also predict a difference in growth rate between males and females in species exhibiting sexual dimorphism. To be consistent with competition theory (Newton 1979), single nestlings should grow fastest as food and care is undivided while larger broods grow slowest.

## Study Area

Our study was conducted from 1998-99 in the mountains of west-central Idaho. The study area encompassed portions of the Boise, Payette, Snake, and Salmon River drainages where elevations range from 460 to 3,050 m (Steele et al. 1981). The study area was mostly administered by USFS, however state and private lands also occurred throughout Washington, Adams, Idaho, Valley, and Boise counties.

The study area is a mix of lowland meadow, rangeland and mid to higher-elevation mixed coniferous forests. The spruce-fir zone occurs at higher elevations throughout the area and is dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) (Steele et al. 1981). The ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudostsuga menziesii*) zones are more common at mid to lower-elevations (Steele et al. 1981) and in addition to ponderosa pine and Douglas-fir include grand fir (*Abies grandis*), western larch (*Larix occidentalis*), and lodgepole pine in cool air drainages and frost pockets (Steele et al. 1981). Common understory species include mountain maple (*Acer glabrum*), ninebark (*Physocarpus malvaceus*), blue huckleberry (*Vaccinium globulare*), snowberry (*Symphoricarpos* spp.), and white spirea (*Spirea betulifolia*). Highest precipitation is typically recorded in December and January. Snow accumulation can exceed 10 m in some northwestern parts of Adams and Valley counties (State Climate Services 1999). Minimum winter temperatures drop below -18° C and summer temperatures can reach 38° C (State Climate Services 1999).

## Methods

Climate data used in this study were compiled from eight weather stations across the study area ranging from 808 to 1,802 m above sea level. This elevation band was representative of goshawk locations at the lower to mid-elevations.

We searched for breeding goshawks and nests from March to August of 1998 and 1999 in both historical territories and new areas. A territory is

defined as the spatial extent of the area used by male, female, and young goshawks during the breeding season. Search effort was concentrated more heavily in historical breeding territories, therefore our search results are biased towards previously occupied sites. Search techniques included listening for courtship or other adult vocalizations (Penteriani 1999), call playbacks (Kennedy and Stahlecker 1991, Bosakowski and Vaughn 1996), and searching for nests, goshawk excrement, feathers, or prey plucking posts (Fuller and Mosher 1987). We recorded vocalizations and feathers of other raptors found in the search area. We took all reasonable precautions to limit our disturbance in nest areas during all stages of the nesting season. Frequent and lengthy nest visits during the prelaying period were avoided as recommended by Fyfe and Olendorff (1976). After egg laying, we entered nest areas only to determine presence or absence of females.

A territory was considered occupied if a female goshawk or fresh greenery sprigs were present on a goshawk nest (Hanauska-Brown 2000). A historical territory was considered unoccupied if no goshawk breeding behaviors or activities were documented at historical nests or in other nesting areas in proximity to historical nests. An occupied territory was considered successful only if at least one nestling reached 80% of fledging age (Steenhof 1987). All occupied territories found post-fledging were considered successful. Nestling age was estimated using a photographic guide (Boal 1994). Although aging goshawk nestlings using a photographic guide is subjective, all observers were trained in application of the guide. Also, multiple visits to the same nest provided an opportunity to follow nestling development through photographs of the different stages (Boal 1994) thereby indirectly confirming the age of the previous visit. Estimates of a 35-day incubation period and 41-day nestling period (Newton 1979) were used to back-date the approximate time of egg laying. We climbed to nests as soon as possible after hatching to confirm the hatch date estimates that were based on back-dating and nesting adult behavior. We calculated productivity in two ways: 1) number of fledged young per nest and 2) number of fledged young per successful nest. We omitted nests found after young had fledged from productivity estimates, as including these nests and young tends to underestimate productivity (Steenhof 1987).

Nestling growth was calculated for individual nestlings and per nest in 1999 only. The first weight was collected within five days of hatching when possible and three to four more weights were collected until nestlings reached 35 days of age. We climbed to nests to collect the first weight after female behavior or sign around the nest (Schnell 1958, Boal 1994) indicated the eggs had hatched. Nestlings were weighed with spring scales, individually marked with plastic zip ties on either or both legs, and later banded with individually-numbered USGS bands. Crop and gut contents were not adjusted for as most climbing was done before the morning feeding or mid-day after some digestion had occurred. Full crops were noted in some individuals, however, the influence of a full crop was minimized as we calculated a trend in growth, not grams gained per day. Growth data were analyzed using Ricklefs' (1967) method of fitting logistic equations to growth curves. We began the growth curve for each nestling at 59 g as the estimated mass at hatching. This initial mass was based on estimates of pre-hatch egg weights (Johnsgard 1990, Newton 1979) and estimates of mass at day-1 (Schnell 1958). A mass of 1007 g was used as the asymptote mass estimate for females and 767 g used as an asymptote mass estimate for males. These asymptote mass estimates were averages of all adult goshawks weighed during this study (23 females and 8 males). Age and weight data were fit to logistic functions that permitted estimation of nestling weights between hatch and fledging. We calculated the growth rate constant, $k$, and the number of days necessary for nestlings to grow from 10 to 90% of their fledging mass. This is the approximately linear portion of the logistic curve (Ricklefs 1967) when nestling goshawks are between 4 and 37 days of age.

We hypothesized that individuals within a nest would exhibit different growth rates based on asynchronous hatching, sibling competition, and sexual dimorphism (Lack 1954, Bechard 1983, Bortolotti 1989, Koga et al. 1989). We also hypothesized mean growth rates among nests would differ based on differences in energy consumption determined by adult condition or habitat quality (Quinney et al. 1986, Bortolotti 1989). We tested for a difference in growth rate between all male and all female nestlings using a standard $t$-test (Zar 1996) to rule out nestling gender as a factor in among nest comparisons. We evaluated difference

in mean growth among nests using a test on the significance of the linear regression coefficient (Sokal and Rohlf 1981).

This test is a t-statistic and if significant ($P \leq 0.05$), there is evidence that the regression coefficent significantly deviates from zero (Sokal and Rohlf 1981).

## Results

We monitored 18 occupied territories in 1998 and 28 in 1999. Eleven of these nests were located in new territories. The remaining 35 nests were associated with historical territories, where occupancy was >35% for both years (14 of 33 visited historical territories occupied in 1998 and 21 of 35 in 1999). In eight historical goshawk nests, we found species other than goshawks. They included three great horned owls, one long-eared owl (*Asio otus*), one Cooper's hawk, one sharp-shinned hawk (*Accipiter striatus*), one common raven (*Corvus corax*), and one flying squirrel (*Glaucomys sabrinus*). Great horned owl feathers were located within 25 m of at least 10 goshawk nest trees. Barred owls (*Strix varia*) were heard in five historical territories. In one of these territories, owls, but no goshawks, were observed in both 1998 and 1999. Conversely, in two territories, barred owls were heard early in the nesting season 100 m from goshawk nests that successfully fledged young.

Nine of 46 (20%) occupied territories where eggs were laid failed. There was no significant difference between failure rates in 1998 and 1999 (17% and 21%). Seven nests failed during the incubation stage and two failed during the nestling stage. The reasons for failure at two nests were adult depredation and nestling depredation by great horned owls. Suspected reasons of failure or nestling loss in other areas included predation, siblicide, and human disturbance. One nestling disappeared from a nest with no sign of predation in the surrounding area. The plucked remains of a nestling from a different territory were found directly beneath the nest where a second nestling remained. Three nests were located within 50 m of periodic human disturbance (e.g. road or fence construction). One female nestling from a brood of two was removed by a falconer, the remaining nestling fledged at a later date.

The mean egg laying date in 1998 ($n = 8$) and 1999 ($n = 17$) was 29 and 26 April (range = 10 April – 15 May). The mean hatching date in 1998 was 3 June and in 1999 it was 31 May (range = 15 May – 19 June), and the mean fledging date was 14 July in 1998 and 11 July in 1999 (range = 25 June – 30 July). Egg laying, hatching, and fledging dates given are estimates only, based on backdating from nestling appearance and fledging date.

In 1998, the mean number of fledged young per occupied territory was 1.5 ($n = 11$, range = 0 - 4), and the mean number per successful territory, where at least one young fledged was 2.1 ($n = 8$, range = 1 - 4). In 1999, the number of fledged young per occupied territory was 1.5 ($n = 23$, range = 0 - 3) and the number per successful territory was 2.0 ($n = 17$, range = 1 - 3). There was no significant difference in productivity between years.

We collected growth data from 13 female and 11 male nestlings at 12 nests during 1999. Climbing nest trees to collect these data began 31 May and ended 11 July. The age of 24 weighed young ranged from 3 to 32 days and the weights ranged from 40 to 1,000 g (Figure 1). The mean $k$ value for female nestlings was $0.19 \pm 0.01$ and the mean for male nestlings was $0.18 \pm 0.01$. The mean number of days to reach 90% of fledging mass for females and males was $24.6 \pm 1.36$ days, and $25.4 \pm 1.37$ days. There was no significant difference between male and female growth rates in $k$ value or in number of days to reach 90% of fledging mass. When growth data were pooled by nest, variability among the 12 nest sites became apparent. Mean growth per nest ranged from 17 to 33 days to reach 90% of fledging mass. Nestlings from the same nest generally grew at similar rates, but growth rates among nests differed ($P < 0.01$) (Figure 2).

Only 3 of the 12 nests monitored had a brood size of greater or less than two. Mean growth rates in the two nests with three nestlings ($k = 0.17$ and 0.20) and the nest with only one nestling ($k = 0.19$) were intermediate within the range of all nests ($n = 12$, $k$-range = 0.13 – 0.27) (Figure 2).

## Discussion

Historical nest occupancy in the west-central Idaho study site was >35% in both 1998 and 1999. We did find six other species using historical nests including four raptor and one mammal species. Presence of other raptor species in goshawk nest stands in this study did not appear to prohibit goshawk nesting activity, however, goshawk

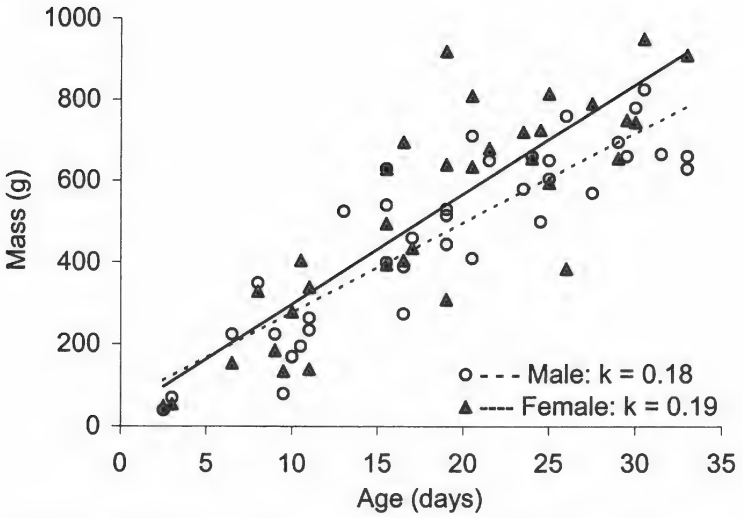


Figure 1. Mass (g) and corresponding ages (days) for 13 female and 11 male northern goshawk nestlings measured during 1999 in west-central Idaho.

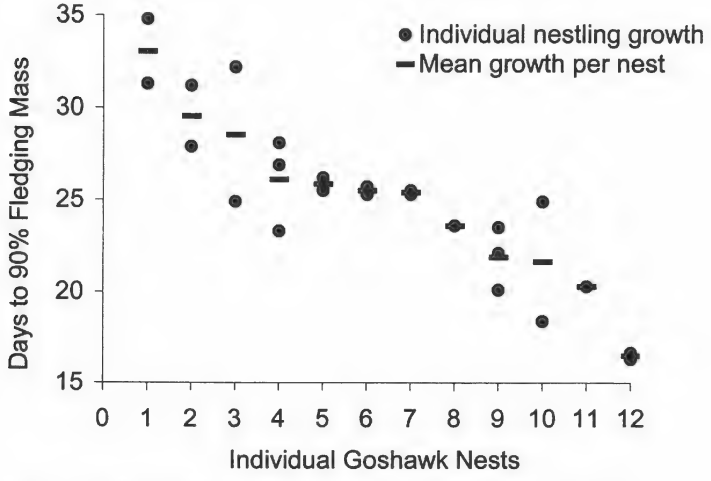


Figure 2. Individual nestling growth in days, and mean growth within 12 northern goshawk nests monitored during 1999 in west-central Idaho.

productivity and survival were negatively affected. Consistent with the findings of other research (Boal and Mannan 1994), we documented great horned owl predation of an adult female goshawk, at least three nestlings, and three fledglings. Barred owl range expansion (Sharp 1989, Wright and Hayward 1998) into Idaho may also detrimentally affect goshawk productivity and should be further investigated. Bent (1937) reported a barred owl killing a goshawk, and Sadler (1993) reported sightings of both species in the same locality during the breeding season. We did not witness any interactions between these species, nor did we see goshawks respond to nearby calling barred owls.

Twenty percent of the nests failed in territories where eggs were laid. There were no signifi-

cant between year differences in nest success, number of young fledged per occupied territory, or number of young fledged per successful territory. Nest success calculations can be influenced by timing of nest searching. We searched for nests from March through August, and all failures were of nests located during the incubation stage. This is consistent with Widén (1985) who found goshawk nests most often failed before or soon after egg laying. We also had less time to document failures at nests found later in the nesting period. We felt our activities during the incubation stage did not affect nest success as we limited our visits and disturbance. Rather, nest success appeared more closely associated with predation and anthropogenic disturbance unrelated to our activities.

Mean egg laying, hatching, and fledging dates were four days later in 1998 than in 1999 in west-central Idaho. Snow remained longer and deeper into April and May 1999 (i.e., +20.3 cm in April, and +4.1 cm in May), yet total precipitation was higher during spring (March–May) 1998 by an average of 15.2 cm (National Climate Data Center 1999). Mean monthly temperatures were also higher during spring 1998 by an average of 1.2°C (National Climate Data Center 1999), potentially reducing any negative effects of increased precipitation. Mean egg laying, hatching, and fledging date estimates for goshawks in west-central Idaho were within the range of dates reported in other studies from the northwestern United States (Bull and Hohmann 1994, DeStefano et al.1994, Patla 1997, Finn 2000). Our results indicate that goshawk nesting chronology for the northwestern United States is predictable and thus should guide survey design and implementation of management prescriptions.

Nest productivity of goshawks in our study was also similar to other studies in the northwestern United States (Table 1). Habitat conditions of nesting areas in west-central Idaho were generally similar to conditions reported in other northwestern studies (i.e., mixed coniferous stands with trees of medium to large size, and medium to high density canopies). Factors influencing occupancy and productivity were similar to other studies as well. Anecdotally, we observed the effects of human disturbance (e.g., road construction, falconry) at the nest area and habitat alteration (e.g., road and fence construction) on a territory scale. These observations emphasize the importance of understanding factors at multiple scales when drawing conclusions from productivity data.

Male and female nestling growth rates were not significantly different, nor were within nest growth rates. Mean growth rates among nests did differ (Figure 2). Nestling growth rates have not been calculated for goshawks in other studies. Although goshawk growth curves from the Sierra Nevada (Schnell 1958) resemble our growth curves, Schnell did not calculate slopes or $k$ values. We expected female and male nestling growth rates to differ based on their sexual dimorphism and the hypothesis that variable growth can be explained by adult body size (Ricklefs 1973). Our ability to detect a difference may have been hindered by small sample sizes or the differences in growth rates observed among nests (Figure 2). We also expected slower growth in goshawks when compared to growth of Cooper's hawks due to

TABLE 1. Northern goshawk productivity estimates (fledglings/occupied nest and fledglings/successful nest) from this west-central Idaho study, eastern Idaho[a], Washington [b], Oregon[c], and northern California[d].

| Source | Occupied Nest | | Successful Nest | |
|---|---|---|---|---|
| | $n$ | Mean | $n$ | Mean |
| This study | 34 | 1.5 | 25 | 2.1 |
| Patla 1997[a] | 68 | 2.0 | 62 | 2.1 |
| Finn 2000[b] | 12 | 1.2 | 8 | 1.9 |
| DeStefano et al. 1994[c] | 6 | 2.2 | | |
| | 10 | 1.9 | | |
| | 9 | 1.0 | | |
| Reynolds and Wight 1978[c] | 48 | 1.7 | | |
| Bull and Hohmann 1994[c] | 12 | 1.2 | 10 | 1.4 |
| Woodbridge and Detrich 1994[d] | 84 | 1.9 | 73 | 2.2[1] |

[1]Estimate from data presented.

differences in adult body size. Our estimate for male goshawk growth was lower than that reported for male Cooper's hawks, but our estimate for female goshawk growth was identical to that reported for female Cooper's hawks (Sumner 1929). A legitimate test of the 'variable growth due to body size' hypothesis (Ricklefs 1973) would include standardization of breeding territory habitat conditions, adult health and adult experience.

We expected single nestlings to grow fastest since food and care were undivided. We also expected larger broods (i.e., broods of three in this study) to grow the slowest because of increased competition. Though qualitative, our observations contradicted both expectations. Growth rates for broods with one or three nestlings were intermediate to growth rates measured on broods with two nestlings (Figure 2). Only three of the 12 nests we monitored had a brood size different from two and thus we could not statistically assess the effect of brood size on nestling growth. Our observations are consistent with Bortolotti (1989) and Schaadt and Bird (1993) as they detected no effect of brood size in bald eagle or osprey (*Pandion haliaetus*) nestling growth.

In our study, nestling growth rates differed by nest, but not between the sexes or between individuals within the same nest. Similar findings were reported by Schaadt and Bird (1993) and White and Brisbin (1980), who failed to detect significant within brood differences in male and female growth rates of osprey and barn owls (*Tyto alba*). The differences in nestling growth rates among nests in our study may have been genetically determined (White and Brisbin 1980) or related to differences in energy consumption by nestlings. Bortolotti (1989) and Bechard (1983) implied energy consumption, as related to habitat condition and adult foraging abilities, was the most important determinant of nestling growth. Our results support this theory and suggest that energy consumption, specifically prey deliveries to the nest, may be the primary determinant of goshawk nestling growth. Thus, in west-central Idaho, goshawk nestling growth may offer a reasonable index to habitat quality and adult condition at individual breeding territories during the nestling season.

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## Literature Cited

Beals, J. W., and C. E. Harris. 1996. Northern goshawk nest area monitoring in the Twin Falls Ranger District of the Sawtooth National Forest. Unpublished report on file at Idaho Fish and Game, Boise, Idaho.

Bechard, M. J. 1983. Food supply and the occurrence of brood reduction in Swainson's hawk. Wilson Bulletin 95:233-242.

Beier, P., and J. E. Drennan. 1997. Forest structure and prey abundance in foraging areas of northern goshawks. Ecological Applications 7:564-571.

Bent, A. C. 1937. Life histories of North American birds of prey. Part One, US National Museum Bulletin. Washington, D.C.

Boal, C. W. 1994. A photographic and behavioral guide to aging nestling northern goshawks. Studies in Avian Biology 16:32-40.

Boal, C. W., and R. W. Mannan. 1994. Northern goshawk diets in ponderosa pine forests on the Kaibab Plateau. Studies in Avian Biology 16:97-102.

Bortolotti, G. R. 1989. Factors influencing the growth of bald eagles in north central Saskatchewan. Canadian Journal of Zoology 67:606-611.

Bosakowski, T., and M. E. Vaughn. 1996. Developing a practical method for surveying northern goshawks in managed forests of the western Washington Cascades. Technical note. Western Journal of Applied Forestry 11:109-113.

Bull, E. L., and J. E. Hohmann. 1994. Breeding biology of northern goshawks in northeastern Oregon. Studies in Avian Biology 16:103-105.

Crocker-Bedford, D. C. 1990. Goshawk reproduction and forest management. Wildlife Society Bulletin 18:262-269.

Crocker-Bedford, D. C. 1998. The value of demographic and habitat studies in determining the status of northern goshawks (*Accipiter gentilis atricapillus*) with special reference to Crocker-Bedford (1990) and Kennedy (1997). Journal of Raptor Research 32:329-336.

DeStefano, S., S. K. Daw, S. M. Desimone, and E. C. Meslow. 1994. Density and productivity of northern goshawks: Implications for monitoring and management. Studies in Avian Biology 16:88-91.

Doyle, F. I., and M. N. Smith. 1994. Population responses of northern goshawks to the ten year cycle in numbers of snowshoe hares. Studies in Avian Biology 16:122-129.

Finn, S. P. 2000. Multi-scale habitat influences on northern goshawk occupancy and reproduction on Washington's Olympic Peninsula. M.S. Thesis, Boise State University, Boise, Idaho.

Fuller, M. R., and J. A. Mosher. 1987. Raptor survey techniques. Pages 37-65 *In* B. G. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird (editors), Raptor management techniques manual. Science and Technical Series, no. 10, National Wildlife Federation. Washington, D.C.

Fyfe, R. W., and R. R. Olendorff. 1976. Minimizing the dangers of nesting studies to raptors and other sensitive species, paper 23. Unpublished report on file at Canada Wildlife Service, Ottawa.

Hanauska-Brown, L. A. 2000. Evaluation of northern goshawk (*Accipiter gentilis*) productivity, nestling growth, and adult health in relation to a central Idaho habitat potential model. M.S. Thesis, Boise State University, Boise, Idaho.

Johnsgard, P. A. 1990. Hawks, eagles, and falcons of North America: biology and natural history. Smithsonian Institute Press, Washington, D.C.

Kennedy, P. L. 1997. The northern goshawk (*Accipiter gentilis*): is there evidence of a population decline? Journal of Raptor Research 31:95-106.

Kennedy, P. L., and D. W. Stahlecker. 1991. Broadcast of calls of the northern goshawk: their effectiveness and their use in inventory and long-term monitoring programs. Eagle Environmental Report. USDA Forest Service, Albuquerque, New Mexico.

Koga, K., S. Shiraishi, and T. A. Uchida. 1989. Growth and development of the black-eared kite (*Milvus migrans lineatus*). Japanese Journal of Ornithology 38:31-42.

Kostrzewa, R., and A. Kostrzewa. 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian kestrels, common buzzards, and northern goshawks. Auk 108:342-347.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford University Press, London.

National Climate Data Center. 1999. National Oceanic and Atmospheric Administration, Asheville, North Carolina. Available online at http://www.ncdc.noaa.gov.

Newton, I. 1979. Population Ecology of Raptors. T. & D. Poyser, London.

Patla, S. M. 1997. Nesting ecology and habitat of the northern goshawk in undisturbed and timber harvest areas on the Targhee National Forest, greater Yellowstone ecosystem. M.S. Thesis, Idaho State University, Pocatello, Idaho.

Penteriani, V. 1997. Long-term study of goshawk breeding population on a Mediterranean mountain (Abruzzi Apennines, central Italy): Density, breeding performance and diet. Journal of Raptor Research 31:308-312.

Penteriani. V. 1999. Dawn and morning goshawk courtship vocalizations as a method for detecting nest sites. Journal of Wildlife Management 63:511-516.

Quinney, T. E., D. J. T. Hussell, and C. D. Ankey. 1986. Sources of variation in growth of tree swallows. Auk 103:389-400.

Reynolds, R. T., S. M. Joy, and D. G. Leslie. 1994. Productivity, fidelity, and spacing of northern goshawks in Arizona. Studies in Avian Biology 16:106-113.

Reynolds, R. T., and H. M Wight. 1978. Distribution, density, and productivity of accipiter hawks in Oregon. Wilson Bulletin 90:182-196.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 49:978-983.

Ricklefs, R. E. 1969. Preliminary models for growth rates of altricial birds. Ecology 50:1031-1039.

Ricklefs, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 2:177-201.

Ross, H. A. 1980. Growth of nestling Ipswich sparrows in relation to season, habitat, brood size, and parental age. Auk 97:721-732.

Sadler, D. 1993. Barred owl and northern goshawk co-occurrence. Ontario Birds April:35.

Schaadt, C. P., and D. M. Bird. 1993. Sex-specific growth in ospreys: the role of sexual size dimorphism. Auk 110:900-910.

Schnell, J. H. 1958. Nesting behavior and food habits of goshawks in the Sierra Nevada of California. Condor 60:377-403.

Sharp, D. U. 1989. Range extension of the barred owl in western Washington and first breeding record on the Olympic Peninsula. Journal of Raptor Research 23:179-180.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The Principles and Practice of Statistics in Biological Research. Second edition. W. H. Freeman and Company, New York.

Squires, J. R., and R. T. Reynolds. 1997. Northern goshawk (*Accipiter gentilis*). *In* A. Poole and F. Gill (editors), The Birds of North America, no. 298. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington D.C.

Squires, J. R., S. H. Anderson, and R. Oakleaf. 1991. Prairie falcons quit nesting in response to spring snowstorm. Journal of Field Ornithology 62:191-194.

State Climate Services. 1999. Biological and Agricultural Engineering Department, University of Idaho, Moscow, Idaho. Available online at http://snow.ag.uidaho.edu.

Steele, R., R. D. Phister, R. A. Ryker, and J. A. Kittams. 1981. Forest habitat types of central Idaho. USDA Forest Service, General Technical Report INT-114, Ogden, Utah.

Steenhof, K. 1987. Assessing raptor reproductive success and productivity. Pages 157-170 *In* B. G. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird (editors), Raptor management techniques manual. Science and Technical Series, no. 10 National Wildlife Federation. Washington, D.C.

Sumner, E. L. 1929. Comparative studies on the growth of young raptors. Condor 31:85-111.

USDA Forest Service. 1990. Title 2600 – Wildlife, fish, and sensitive plant habitat management. USDA Forest Service, Amendment Number 2600-90-1, Washington, D.C.

USDA Forest Service. 2000a. Boise National Forest. Draft land management plan. USDA Forest Service, Boise, Idaho.

USDA Forest Service. 2000b. Payette National Forest. Draft land management plan. USDA Forest Service, Intermountain Region, McCall, Idaho.

Ward, J. M., and P. L. Kennedy. 1996. Effects of supplemental food on size and survival of juvenile northern goshawks. Auk 113:200-208.

White, G. C., and I. L. Brisbin, Jr. 1980. Estimation and comparison of parameters in stochastic growth models for barn owl. Growth 44:97-111.

Widén, P. 1985. Breeding movements of goshawks in boreal forest in Sweden. Holarctic Ecology 8:273-279.

Widén, P. 1989. The hunting habitats of goshawks (*Accipiter gentilis)* in boreal forests of central Sweden. Ibis 131:205-213.

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Widén, P. 1997. How and why, is the goshawk (*Accipiter gentilis*) affected by modern forest management in Fennoscandia? Journal of Raptor Research 31:107-113.

Woodbridge, B., and P. J. Detrich. 1994. Territory occupancy and habitat patch size of northern goshawks in the southern Cascades of California. Studies in Avian Biology 16:83-87.

Wright, A. L., and G. D. Hayward. 1998. Barred owl range expansion into the central Idaho wilderness. Journal of Raptor Research 32:77-81.

Younk, J. V., and M. Bechard. 1994. Ecology of the northern goshawk in high elevation aspen forest of northern Nevada. Studies in Avian Biology 16:119-121.

Zar, J. H. 1996. Biostatistical Analysis, third edition. Prentice Hall, Upper Saddle River, New Jersey.

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# Structure, Abundance, and Movements of an Allacustrine Population of Rainbow Trout in the Naknek River, Southwest Alaska

## Abstract

Allacustrine rainbow trout move downstream from Naknek Lake into the Naknek River to spawn, and become vulnerable to angling during the spawning season. Regulations, including an annual angling closure from 10 April through 7 June, have been implemented to protect spawning fish from angling mortality, but the synchrony of the angling closure to the time when sexually mature fish are present in the river was unknown. We describe (1) the length structure and abundance of sexually mature fish in the spawning population and (2) the post-spawning movements of sexually mature fish. We sampled sexually mature fish ranging from 424 to 860 mm fork length during 2000 and 2001. The spawning population was estimated to be ~ 3,000 fish. Of 70 radio-tagged fish, 80% moved from the river to the lake by 8 June 2001, but several fish remained in the river throughout the summer. More than half of the radio-tagged fish that moved to the lake returned to the river during the fall and early winter. A substantial portion of the spawning population was protected by the annual angling closure, but some fish were not protected because they remained in the river through the summer or returned to the river before it froze in the fall.

## Introduction

Rainbow trout (*Oncorhynchus mykiss*) have a broad natural range in western North America extending north to the Kuskokwim River, Alaska (Behnke 1992). An unusual migration pattern among rainbow trout involves allacustrine movements or the migration of sexually mature fish that reside in a lake to the lake outlet for spawning (Northcote 1997). Such a migration pattern has been described among rainbow trout populations in British Columbia (Lindsey et al. 1959; Hartman et al. 1962; Northcote 1962, 1969) and Alaska (Minard et al. 1992), but information on the dynamics of these populations is limited. The allacustrine populations in British Columbia and Alaska tend to be composed of large, long-lived fish that are associated with large lakes with abundant prey fishes (Cartwright 1961, Minard and Dunaway 1991, Minard et al. 1992, Riffe 1994). The common prey species in these lakes is anadromous sockeye salmon (*Oncorhynchus nerka*) or kokanee, i.e., sockeye salmon that reside in freshwater systems through their life cycle (Burgner et al. 1969, Gwartney and Burger 1986, Dunaway and Sonnichein 2001).

Fisheries biologists need to know the population characteristics and movement patterns of allacustrine rainbow trout to manage populations. Because the large, sexually mature individuals within populations that display this migratory pattern become highly concentrated during the spawning period, they are particularly vulnerable to exploitation by anglers. Understanding the extent and timing of allacustrine movements by spawning populations can provide insight into the potential effectiveness of regulations designed to protect spawning fish from angling mortality.

Our goal was to describe selected aspects of the dynamics of the allascustrine population of rainbow trout that spawns in the Naknek River, Southwest Alaska. Our objectives were to describe (1) the length structure and abundance of sexually mature fish in the spawning population and (2) the post-spawning movements of sexually mature fish. The findings provide insight as to the potential effectiveness of special regulations for rainbow trout on the Naknek River designed to protect spawning fish from excessive exploitation as well as the

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physiological stress or latent mortality associated with being caught and released.

## Study Area

Rainbow trout that spawn in the Naknek River of Southwest Alaska are believed to carry out allacustrine migrations, moving downstream from Naknek Lake to spawn in the Naknek River during the spring then returning to the lake. Rainbow trout in the spawning population are large with total lengths up to 920 mm total length (TL). They concentrate in a short reach of the Naknek River during the spring spawning period making them highly vulnerable to angling. Consequently, the Alaska Department of Fish and Game manages the Naknek River for trophy rainbow trout and protects the spawning population with a complete angling closure from 10 April to 7 June. Special regulations apply during the angling season: a maximum length limit of 45 cm TL, a creel limit of 1 fish/d from 8 June through 31 October and 5 fish/d from 1 November through 9 April, and use of only single-hook lures by anglers. The synchrony of the closure relative to the time when sexually mature fish are present in the river was unknown.

The Naknek River is near the northern limit of the natural range of rainbow trout (Behnke 1992). The river is formed by the outlet from Naknek Lake and flows past the town of King Salmon into Bristol Bay of the Bering Sea (Figure 1). Rainbow trout spawn within the upstream 14 km of the river that is not influenced by tides. Within this 14-km segment, rainbow trout spawning is concentrated in the downstream half where gravel bars and riffles are abundant. Discharge from Naknek Lake into the river is stable during the spawning period and rises gradually during late spring and early summer as snow melts in the mountains and contributes runoff into the lake.

Naknek Lake is oligotrophic with a surface area of ~ 610 $km^2$ and a maximum depth of 173 m (Burgner et al. 1969). Most of the lake is relatively turbid due to runoff from glaciers carried by the Savonoski River, with the exception of the Bay of Islands area (Figure 1).

Rainbow trout spawn in four streams around Naknek Lake: Idavain Creek, American Creek, Brooks River, and Naknek River. Mixing of rainbow trout from the Brooks River, Idavain Creek, and Naknek River within Naknek Lake during the nonspawning period has been identified by tagging studies. In addition to rainbow trout, the Naknek River drainage supports sockeye salmon, chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and pink salmon (*O. gorbuscha*), also Dolly Varden (*Salvelinus malma*), Arctic char (*S. alpinus*), lake trout (*S. namaycush*), Arctic grayling (*Thymallus arcticus*), and northern pike (*Esox lucius*). Sockeye salmon smolts are believed to be the primary prey for rainbow trout in the system.

## Methods

### Length Structure

Sampling was conducted over the upstream 14 km of the Naknek River (Figure 1). This segment of river was divided into four contiguous reaches of approximately equal length for sampling. All four reaches were sampled in 2000, but only the two downstream reaches were sampled in 2001 because almost all of the spawning habitat was in those two reaches. Sampling occurred at least 5 d each week from 20 March to 20 May 2000 and from 10 to 28 April 2001. Rainbow trout were captured with beach seines, drifting gill nets, and hook and line. The beach seine was 45.7 x 5.4 m with 2.54-$cm^2$ knotless nylon mesh, a lead line, and a float line. It was deployed by backing a boat from the shore and allowing it to drift downstream. The boat was used to move the outer end to the shore where the seine was retrieved from each end. The gill net was 15.2 x 3.0 m with 5.1-$cm^2$ multifillament mesh, a lead line, and a float line. The gill net was deployed so that it would drift with the current. When fish were entangled, the net was retrieved. Hook-and-line sampling was conducted by back trolling with diving lures and by fly fishing with an assortment of large, black streamers. Back trolling was conducted from a boat with a slow drift controlled by the power of an outboard motor. Diving lures were fished 5-10 m downstream as the boat moved slowly downstream.

Captured rainbow trout were measured to the nearest millimeter fork length (FL), categorized as sexually immature or mature, and the sex of sexually mature fish was determined. Sexually immature fish lacked secondary sexual features, whereas sexually mature fish were those fish believed to be capable of spawning during the spring of capture. Sexually mature males were dark, had

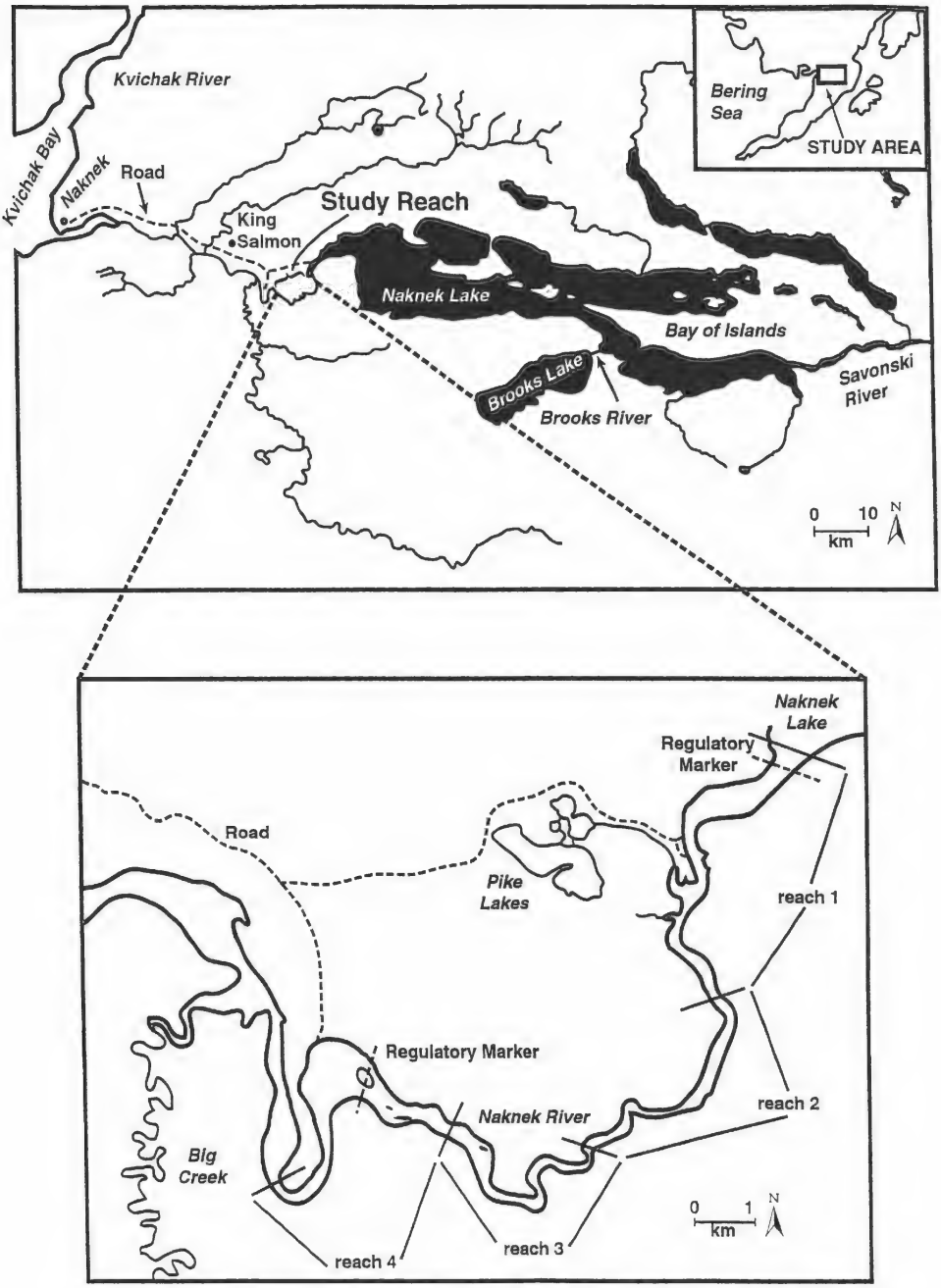


Figure 1. The study area is within the Naknek River watershed and southwest Alaska with the locations of the four sampling reaches.

a well-developed kype, and often exuded milt. Sexually mature females were silver, lacked a kype, had an extended abdomen with an ovipositor protruding from the vent, and sometimes exuded eggs. Differences between classes in the mean lengths of sexually mature fish were assessed using a two-sample *t*-test. Significance was determined at $P \leq 0.05$.

An individually numbered Floy T-Anchor tag, model FS-94, was inserted in the left side near the posterior base of the dorsal fin, a fin was clipped, and the fish were released near the point of capture. Markings enabled recaptured fish to be excluded from the data set describing population structure and allowed us to estimate abundance.

### Abundance

A multiple mark-recapture technique was used to estimate the abundance of spawning rainbow trout. A capture history for each marked fish was created indicating the weeks during which each fish was marked and recaptured in order to model capture probabilities (Nichols 1992). Capture probabilities can vary due to time or trapping occasion (model $M_t$), behavioral responses (model $M_b$), variation among individual animals or heterogeneity (model $M_h$), or combinations of these factors (models $M_{tb}$, $M_{th}$, $M_{bh}$, and $M_{tbh}$) (Otis et al. 1972). The program CAPTURE was used to compute estimates of abundance from the capture histories (Rexstad and Burnham 1991). Likelihood-ratio and goodness-of-fit tests were used to identify the most appropriate model. Capture probabilities varied over time and among individual animals, so model $M_{th}$ was used to estimate the abundance of spawning rainbow trout.

### Movements

Post-spawning movements were assessed in 2001 using radio telemetry. Transmitters had frequencies of 152.610-153.990 Mhz, weighed 19 g, had a maximum life span of 1 yr, and were equipped with a mortality sensor that was activated by lack of movement for 8 hr. Transmitters were surgically implanted in the body cavity using the shielded-needle technique (Ross and Kleiner 1982) and surgical procedures of Summerfelt and Smith (1990). Transmitter weight was substantially less than 2% of fish weight (Winter 1996). Capture and implantation were conducted shortly after the fish completed spawning using fish captured in reach 4 (Figure 1). A beach seine, drifting gill net, or hook and line were used to capture spawned-out females and spawning males beginning 10 April 2001 and continuing for 5 wk. The number of fish implanted with transmitters during each week was based on the proportion of spawned-out fish sampled over that time period in 2000. The goal for transmitter implantations was 6, 10, 15, 30, and 13 fish each week, with approximately equal numbers of males and females. Our total sample-size goal was 74 fish, based on an estimate for a binomial proportion that fish would be in the river or lake on 8 June. We estimated that movements of 61 fish would have to be observed to determine the proportion of immigrants within 12.5% of the true value 95% of the time (Cochran 1997) and adjusting this value to account for 20% fish mortality and transmitter failure between implantation and early June when emigration was anticipated to be complete.

A continuously scanning receiver and data logger were placed near the regulatory marker at the lake outlet (Figure 1) to detect movement of radio-tagged fish from the river into the lake. Two antennas were used to detect the direction of movement of radio-tagged fish. We tracked fish from an airplane at least twice each month from May through December 2001, at an altitude of 500 m over both the lake and river. During each search several passes were made over the river between King Salmon Creek and the lake outlet and occasionally the river was searched downstream to Bristol Bay (Figure 1). The search routine for the lake was concentrated along the shoreline and around islands, and required over 3 hr to complete. The locations of individual radio-tagged fish were recorded with a global positioning system and marked on a map of the river and lake.

## Results

### Length structure

Fork lengths were measured for 820 immature and 892 sexually mature fish ranging from 196 to 830 mm FL in 2000 (Figure 2a). Fork-length measurements were obtained from 229 immature and 661 sexually mature fish ranging from 225 to 860 mm in 2001 when sampling was confined to reaches 3 and 4 (Figure 2b).

The minimum fork length of fish identified as sexually mature was 425 mm in 2000 and 424 in

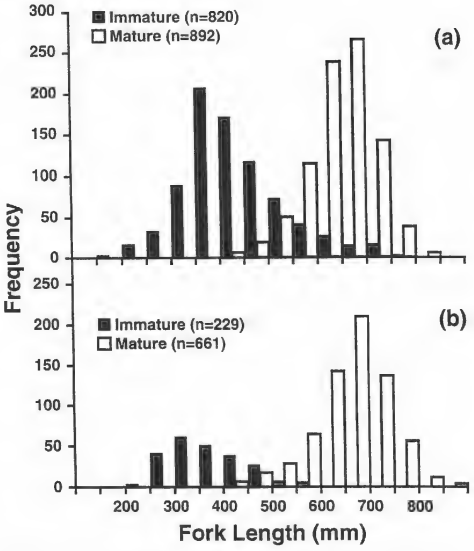


Figure 2. Length frequency distributions of sexually immature and mature rainbow trout captured in the Naknek River, Alaska, in 2000 (a) and 2001 (b).

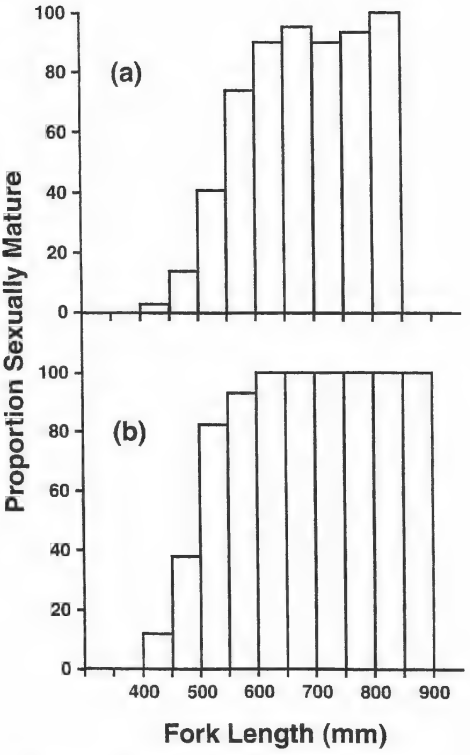


Figure 3. Proportions of sexually mature rainbow trout among length classes captured in the Naknek River, Alaska, in 2000 (a) and 2001 (b).

2001. The proportion of sexually mature fish increased as length increased (Figure 3), but a small proportion of immature fish was observed among even the longest length classes in 2000 when the entire study area was sampled. However, all fish over 650 mm FL were identified as sexually mature in 2001 when only reaches 3 and 4 were sampled.

Sexually mature males tended to be longer than sexually mature females in both 2000 and 2001 (Figure 4). Mean fork lengths of males (676 $\pm$ 2.9 mm) and females (617 $\pm$ 2.7 mm) differed significantly ($P < 0.001$) in 2000. Similarly, mean fork lengths of males (686 $\pm$ 3.7 mm) and females (630 $\pm$ 3.5 mm) differed significantly ($P < 0.01$) in 2001. Males represented 53% of the sexually mature fish sampled in 2000 and 59% in 2001.

## Abundance

Nine, 1-wk capture events took place between 20 March and 21 May 2000 across all four reaches. A total of 983 sexually mature fish were marked with tags and fin clipped, and 115 were recaptured at least once. The first recaptures occurred during the fourth week (10-16 April). The percentage of marked fish increased from week 4 (5.6%) to week 8 (16.2%), but decreased during week 9 (15.1%) to indicate emigration of marked fish from the study area. Thus, week 9 was excluded in the abundance estimate. The estimated number of sexually mature fish in the Naknek River during the 2000 spawning period was 3,258 $\pm$ 389 (95% CI = 2,608-4,143). When limited to data from reaches 3 and 4, abundance was estimated to be 2,484 $\pm$ 429 (95% CI = 1,801-3,511) sexually mature fish.

Three, 1-wk capture events took place between 10 and 30 April 2001 in reaches 3 and 4. A total of 727 sexually mature fish were marked and 77 were recaptured at least once. The proportion of marked fish was 14.2% during week 2 and 12.2% during week 3. The estimated abundance of sexually mature fish in reaches 3 and 4 in 2001 was 2,413 $\pm$ 271 (95% CI = 1,956-3,029), similar to that obtained for the two reaches in 2000.

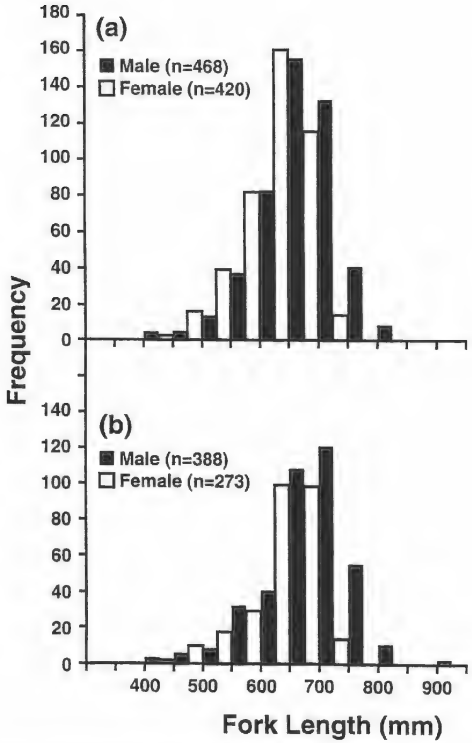


Figure 4. Length frequency distributions of sexually mature male and female rainbow trout captured in the Naknek River, Alaska, in 2000 (a) and 2001 (b).

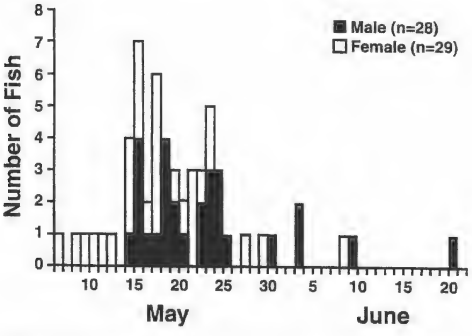


Figure 5. Date and sex of rainbow trout with radio transmitters that moved from the Naknek River to Naknek Lake during the spring 2001.

### Movements

Transmitters were implanted in 38 males (mean FL = 674 ± 9 mm) and 36 females (mean FL = 638 ± 8 mm) between 10 April and 14 May 2001.

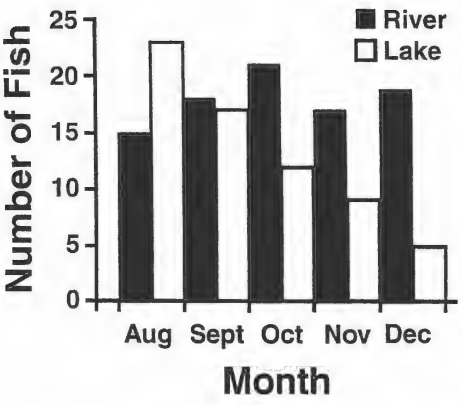


Figure 6. The numbers of rainbow trout with radio transmitters located in either the Naknek River or Naknek Lake from August through December 2001.

As of 8 June, 70 fish (35 of each sex) were alive with functioning transmitters. Of those 70 fish, 56 (27 males and 29 females) had moved from the Naknek River to Naknek Lake by 8 June, and 14 (7 of each sex) remained in the river (Figure 5). Movement to the lake was greatest in the middle of May. All of the fish that moved from the river into the lake did so by 19 June with the exception of one fish that did not enter the lake until 31 August. All of the fish that moved to the lake prior to 13 May were females. The mean fork lengths of males that remained in the river (635 ± 25 mm) and those that moved to the lake (685 ± 9 mm) differed significantly ($P = 0.026$). Similarly, the mean fork lengths of females that remained in the river (592 ± 27 mm) and those that moved to the lake (646 ± 7 mm) differed significantly ($P = 0.010$)

We located 64 radio-tagged rainbow trout during summer; 51 (80%) spent most of the summer in the lake and 13 remained in the river during the summer. Thirty-eight fish were located as of 1 September, 21 (55%) in the lake and 17 in the river. Five of the fish in the river on 1 September had returned to the river after spending the summer in the lake. Between 1 September and 19 December, 11 of the 21 fish in the lake on 1 September returned to the river (Figure 6).

## Discussion

Rainbow trout sampled in the Naknek River in 2000 and 2001 were large, ranging up to 860 mm

FL (Figure 2). Age and growth studies of rainbow trout from the Naknek River (Minard and Dunaway 1991, Riffe 1994) indicated that fish in the spawning population lived up to 13 yr and attained fork lengths of 350-550 mm at age 5 and 550-700 mm at age 10. The minimum length at sexual maturity was 424 mm, but the majority of fish were sexually mature at 551-650 mm FL (Figure 3). Combining information from previous age and growth studies with our observations of lengths at sexual maturity suggest that rainbow trout in the Naknek River become sexually mature at 5-7 yr of age. The sex ratio of fish sampled from the spawning population averaged 56% males over the 2 yr of study. This structure was similar to what has been observed among allacustrine populations in the Kvichak River, Alaska (Steve Fleischman, Alaska Department of Fish and Game, personal communication); Lardeau River-Kootenay Lake, British Columbia (Cartright 1961); and Loon Lake, British Columbia (Hartman et al. 1962).

Length-frequency distributions for rainbow trout captured in the Naknek River during the spawning season showed bimodal patterns distinguishing sexually immature and mature fish (Figure 2). The length frequencies also indicated a low number of mid-length (~ 501-650 mm FL) fish. The low frequency of mid-length fish may have been due to poor recruitment of some cohorts, but it is more likely that sexually immature, mid-length fish reside primarily in Naknek Lake and were not sampled. In the Naknek River the proportion of sexually mature fish increased with downstream progression. Reaches 1 and 2 had little spawning habitat and immature fish were abundant, whereas reaches 3 and 4 had substantial amounts of spawning habitat and sexually mature fish were abundant. Segregation of sexually mature and immature fish during the spawning season is suggested by these observations.

Several > 650 mm FL rainbow trout collected from reaches 1 and 2 in 2000 lacked secondary sexual features and were identified as sexually immature. Consequently, some large fish in the Naknek River during spring were not part of the spawning population.

The estimated number of rainbow trout in the spawning population in the Naknek River was similar to estimates for spawning populations in the Kvichak River, Alaska (2,000-4,500 fish) (Minard et al. 1992) and the outlet of Loon Lake, British Columbia (3,200-7,900 fish) (Hartman et al. 1962), and substantially greater than the numbers in the Lardeau River-Kootenay Lake system (500-700 fish) (Hartman 1969), but the spawning area in the Lardeau River appeared to be much smaller than in the other systems.

Post-spawning movements of rainbow trout observed in the Naknek River indicated than an allacustrine migration occurred among a large proportion (80%) of the fish that spawned in the river (Figure 5). The post-spawning movements from the river to the lake may have been a feeding migration (Northcote 1997). Approximately 1.6 million sockeye salmon spawned in the Naknek River system and tributaries to Naknek Lake in 1999 (Dunaway and Sonnichein 2001), and the lake provides rearing area for the offspring of sockeye salmon that spawn in tributaries to the lake. The post-spawning migration of rainbow trout into Naknek Lake may be a response to the abundance of juvenile sockeye salmon available as food for large rainbow trout. However, rainbow trout that remain in the Naknek River feed on sockeye salmon smolts migrating downstream to Bristol Bay from June through July. Given the abundance of prey fishes in the river, it is not known why large rainbow trout migrate to the lake. Migration to the lake may be an avoidance behavior related to the large influx of adult salmon, most notably sockeye salmon, from June through August. Sockeye salmon become aggressive during spawning and agonistic encounters with rainbow trout are likely to occur (McPhail and Lindsey 1970, Morrow 1980, Groot and Margolis 1991).

Post-spawning female rainbow trout initiated movement into Naknek Lake before males (Figure 5). Females that spawned early tended to leave the river earlier, but males tended to remain in the river through the spawning period. Additionally, both males and females that moved to the lake tended to be larger than those that remained in the river. Rainbow trout that migrate may benefit from the abundant juvenile sockeye salmon prey, fewer aggressive encounters with adult salmon, or lower energy expenditure due to the lack of current in the lake.

Refuge responses among allacustrine salmonids have usually been described as movements to a lake to over-winter (Northcote 1997). However, more than half of the rainbow trout that spawned in the Naknek River and moved into the lake during the summer returned to the river during

the fall and early winter (Figure 6). These returning fish included essentially equal numbers of both sexes. Sexually mature rainbow trout may prefer the river as winter habitat or repeat spawners may stage in the fall for spawning the following spring. Over-wintering in rivers before spawning is common in many steelhead (*O. mykiss*) populations (Withler 1965, Behnke 1992, Begich 1999). Another mechanism that may attract fish to the river in the fall is the abundance of food in the form of deteriorating salmon carcasses.

Most of the rainbow trout that moved to Naknek Lake remained there at least through June and July, and were commonly found in a portion of the lake known as the Bay of Islands (Figure 1). Most of Naknek Lake is glacially turbid during summer due to inflow from the Savonoski River, but there is little or no glacial input by streams flowing into the Bay of Islands. Use of the Bay of Islands by rainbow trout may be due to their ability to more efficiently prey on juvenile sockeye salmon in this area (Gwartney and Burger 1986).

A management implication from this study is that the migration pattern of most of the rainbow trout that spawn in the Naknek River provides them protection from angling because there is little fishing on Naknek Lake. Consequently, fish that migrate to the lake survive longer and grow to large sizes. Spawning fish are protected by an angling closure on the river between 10 April and 7 June, and most of the migrating spawners appear to have moved to the lake by that time. Fish begin to move back to the lake during the fall, but angling on the river subsides in early October when the river freezes. Nevertheless, the segment (~ 20%) of the spawning population that remains in the river through the summer and the fish that return to the river in early fall are protected from harvest and angling mortality by a maximum length limit of 45-cm total length and the use of only single-hook lures by anglers. The combination of allacustrine migration and special regulations on the Naknek River appears to provide substantial protection of the rainbow trout spawning population from excessive angling mortality.

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## Literature Cited

Begich, R. N. 1999. Population ecology of adult steelhead trout (*Oncorhynchus mykiss*) of the Karluk River, Alaska. Master's thesis. University of Idaho, Moscow, Idaho.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6, Bethesda, Maryland.

Burgner, R. L., C. J. Di Costanzo, R. J. Ellis, G. Y. Harry, Jr., H. L. Hartman, O. E. Kerns, Jr., O. A. Mathison, and W. F. Royce. 1969. Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems of southwestern Alaska. Fisheries Bulletin 67:405-459.

Cartwright, J. W. 1961. Investigation of the rainbow trout of Kootenay Lake, British Columbia. British Columbia Fish and Game Branch Management Publication 7, Victoria, British Columbia.

Cochran, W. G. 1977. Sampling techniques, third edition. Wiley, New York.

Dunaway, D. O., and S. Sonnichsen. 2001. Area management report for the recreational fisheries of the Southwest Alaska sport fish management area, 1999. Alaska Department of Fish and Game Fishery Data Series 01-06, Anchorage, Alaska.

Groot, C., and L. Margolis. 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, British Columbia.

Gwartney, L. A., and C. V. Burger. 1986. A radio tagging study of Naknek Drainage rainbow trout. Unpublished Final Report to U.S. Department of Interior, National Park Service, and Alaska Department of Fish and Game, Anchorage, Alaska.

Hartman, G. F. 1969. Reproductive biology of the Gerrard stock rainbow trout. Pages 53-67 *In* T. G. Northcote (editor), Symposium on Salmon and Trout in Streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, British Columbia.

Hartman, G. F., T. G. Northcote, and C. C. Lindsey. 1962. Comparison of inlet and outlet spawning runs of rainbow trout in Loon Lake, British Columbia. Journal of the Fisheries Research Board of Canada 18:173-200.

Lindsey, C. C., T. G. Northcote, and G. F. Hartman. 1959. Homing of rainbow trout to inlet and outlet streams of Loon Lake, British Columbia. Journal of the Fisheries Research Board of Canada 16:695-719.

McPhail, J. C., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada Bulletin 173, Ontario, Canada.

Minard, R. E., and D. O. Dunaway. 1991. Compilation of age, weight, and length statistics for rainbow trout samples

collected in Southwest Alaska, 1954 through 1989. Alaska Department of Fish and Game Fishery Data Series 91-62, Anchorage, Alaska.

Minard, R. E., M. Alexandersdottir, and S. Sonnichsen. 1992. Estimation of abundance, seasonal distribution, and size and age composition of rainbow trout in the Kvichak River, Alaska, 1986 to 1991. Alaska Department of Fish and Game Fishery Data Series 92-51, Anchorage, Alaska.

Morrow, J. E. 1980. The Freshwater Fishes of Alaska. Alaska Northwest Publishing, Anchorage, Alaska.

Nichols, J. D. 1992. Capture-recapture models: using marked animals to study population dynamics. BioScience 42:94-102.

Northcote, T. G. 1962. Migratory behavior of juvenile rainbow trout, *Salmo gairdneri*, in outlet and inlet streams of Loon Lake, British Columbia. Journal of the Fisheries Research Board of Canada 19:201-270.

Northcote, T. G. 1969. Lakeward migration of young rainbow trout (*Salmo gairdneri*) in the upper Lardeau River, British Columbia. Journal of the Fisheries Research Board of Canada 26:33-45.

Northcote, T. G. 1997. Potamodromy in salmonids—living and moving in the fast lane. North American Journal of Fisheries Management 17:1029-1045.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. The Wildlife Society Wildlife Monograph 62, Blacksburg, Virginia.

Rexstad, E., and K. P. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado.

Riffe, R. 1994. Compilation of age, weight, and length statistics for rainbow trout samples collected in Southwest Alaska, 1990-1993. Alaska Department of Fish and Game Fishery Data Series 94-17, Anchorage, Alaska.

Ross, M. J., and C. F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. Progressive Fish-Culturist 44:41-43.

Summerfelt, R. C., and L. S. Smith. 1990. Anesthesia, surgery, and related techniques. Pages 213-272 *In* C. B. Schreck and P. B. Moyle (editors), Methods for Fish Biology. American Fisheries Society, Bethesda, Maryland.

Wilthler, I. L. 1965. Variability in life history characteristics of steelhead trout (*Salmo gairdneri*) along the Pacific Coast of North America. Journal of the Fisheries Research Board of Canada 23:365-393.

Winter, J. D. 1996. Underwater biotelemetry. Pages 555-590 *In* B. R. Murphy and D. W. Willis (editors), Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

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# Diet and Prey Availability of Columbia Spotted Frogs in Northeastern Oregon

## Abstract

Baseline information on the diet and prey availability of Columbia spotted frogs is lacking from most of the species range. Diet was determined from June through October 2002 for 296 frogs in northeastern Oregon. Number of prey items, diet composition, and biomass indices were compared by sex, size classes, water type (ponds versus rivers), month, and study site. Available invertebrates were determined from sticky traps and dip netting in ponds and rivers. A total of 1,299 prey items were identified with an average of 4.4 prey items in each sample (range = 0 - 28). A wide variety of prey were identified including 33 families from 20 orders of invertebrates with only 3 orders representing ≥10% of the composition: beetles (21%), ants/wasps (21%), and flies (10%). Only 14% of the prey were in the larval stages. Female frogs ate about 60% more biomass than males of the same size, presumably because of their need to produce eggs. Biomass of male frog diet samples were greater in rivers than in ponds with a higher percentage of stoneflies, water striders, and beetles. Frogs actively foraged all summer with the highest biomass in September and the lowest in July. Over the summer, composition of spiders, beetles, and flies decreased, while true bugs and ants/wasps increased in the diet. Among study sites, ants/wasps were most abundant at the higher elevations. A higher proportion of invertebrates occurred in the larger sizes in the diet compared with samples of available invertebrates.

## Introduction

Amphibians make up an important component of the aquatic habitats in the Blue Mountains. These species serve as good indicators of overall health of forest and rangeland ecosystems because they depend on water for reproduction, and because their permeable skin makes them particularly sensitive to environmental toxins (Morell 1999). We know relatively little about the biology or the relative health of their populations, particularly with regard to disturbances. Increasing incidence and intensity of fires and other disturbance agents (floods, drought, introduction of fish, habitat alteration, livestock grazing, noxious weed control) in eastern Oregon may threaten these animals and the integrity of the aquatic habitat. Large-scale disturbances such as fire, may have direct and indirect consequences on frogs resulting in predation, loss in habitat, or changes in diet and prey availability.

This study provides basic ecological information on the diet of the Columbia spotted frog (*Rana luteiventris*). This frog species is of interest to managers because it is classified as imperiled by the Oregon Natural Heritage Program, as sensitive by the USDA Forest Service in Region 6, and as a candidate for listing under the Federal Endangered Species Act. Declines in this species have been reported in Yellowstone National Park (Patla and Peterson 1999), Utah (Hovingh 1993), and Nevada (Reaser 2000). The causes of the declines include habitat loss and fragmentation, introduction of predators, cattle grazing, and the loss of natural flood disturbances. Many of these factors could also influence prey availability.

Studies of food habits of the Columbia spotted frog have shown this species to be an opportunistic feeder, taking whatever invertebrates are on, near, or underwater (Turner 1959, Miller 1978, Whitaker et al. 1983) .

Baseline information on diet and prey availability of Columbia spotted frogs is lacking in northeastern Oregon and other portions of its range. This frog typically breeds in permanent ponds but may spend the summer, fall, and winter in ponds or rivers (Bull and Hayes, 2001, 2002). The factors driving the selection of pond or river habitat are not fully known, although diet may be one of several contributing factors. The focus of this study was to compare Columbia spotted frog diet and invertebrate availability between pond and river habitats at six study sites. This study was designed to answer the following five questions: 1) were frogs consuming invertebrates in proportion to their abundance; 2) did frogs select for larger prey items to maximize their energy expenditure foraging; 3) did pond or river habitat provide a greater

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abundance of prey or larger prey items for frogs; 4) was frog diet the same at different study areas; 5) for what duration of the summer did frogs forage and did diet differ?

## Methods

### Study Area

This study was conducted at six sites in two watersheds in northeastern Oregon between June and October 2002 (Table 1). Study areas were selected based on the presence of known breeding sites and previous knowledge of frog movements. Each study site has at least one breeding pond in lentic habitat (Palustrine system) (Cowardin et al. 1979) and an adjacent lotic habitat (Riverine system) within 400 m, except the Rainbow site, which lacks a lotic system. All ponds (lentic) and river habitats (lotic) are in forested habitats and have permanent water in typical years. The breeding ponds range from 60 to 30,000 $m^2$ in size. The earliest breeding activity occurs at the Hohman pond in late March and the latest occurs at Rainbow pond in late April or early May (Table 1). The information on breeding dates was obtained by checking the ponds every 1-2 days after ice melted. Timing of breeding activity at these study sites is a function of elevation, exposure, and temperature of the water source. The ponds at Hohman rarely freeze, while all other pond surfaces typically freeze in November and thaw between March and May.

### Diet Sample

Diet samples were collected every 2 wk from frogs captured in pond and river habitats at the Gun, Starkey, Tailings, and Rainbow study areas. Five percent of frogs captured lacked any stomach contents, and these frogs were not included in the sample. Diet was not determined in two study sites due to difficulty in locating frogs for diet samples. Sampling started in early June after all breeding was completed and ended in mid-October when nighttime temperatures dropped below freezing. Because activity level of arthropods varies with time of day, the order that study sites were sampled was rotated each sampling period.

Frogs were captured with dip nets while I walked along the pond perimeter or river edge at each of the four study sites. Sex and snout-vent length (SVL) were recorded for each frog, and a diet sample was obtained by flushing the stomach of the frog with a catheter (2 mm wide, 56 cm long) attached to a 65-cc syringe inserted through the mouth and esophagus of the frog (Legler and Sullivan 1979, Whitaker et al.1983). Diet samples were preserved in vials of 75% ethanol alcohol and returned to the lab for identification. I assumed the entire diet sample was flushed from the frog because Legler and Sullivan (1979) were confident that they recovered all the material in the stomachs of lizards based on dissection of a few lizards after flushing the stomach; however, no frogs were killed to test this assumption. We attempted to collect five diet samples from the first five frogs captured in both the pond and river at each study site, but limited the time searching for frogs to 2 hr at each site. Food fragments were identified to order or family and categorized into six size classes (1-4.5, 5-9.5, 10-14.5, 15-19.5, 20-24.5, ≥ 25 mm) when enough of the invertebrate was present to estimate size.

Biomass (mg) was determined by oven-drying each sample for 24 hr at 40° C. The largest samples were dried for 48 hr. Because size of frog largely determined the size and amount of prey the frog could consume, I devised an index to standardize for frog size (biomass divided by SVL *100) .

The number of prey items, diet composition, and biomass indices were compared by (1) sex,

TABLE 1. Pond size and depth, dates of breeding, elevation, and location of six study sites used to monitor Columbia spotted frogs in northeastern Oregon, 2002.

| Study Area | Pond size ($m^2$) | Pond depth (m) | Dates of egg laying | Elevation (m) |
|---|---|---|---|---|
| Gun | 887 | 0.8 | 7-17 Apr 02 | 924 |
| Hohman | 300 | 1 | 31 Mar-12 Apr 02 | 935 |
| Starkey | 4,132 | 1.1 | 30 Mar- Apr 98 | 1,001 |
| Whitehorse | 30,000 | 0.7 | 8-14 Apr 02 | 1,188 |
| Tailings | 86-264 | 0.6-2 | 15-25 Apr 02 | 1,380 |
| Rainbow | 28,526 | 3 | 12-28 May 02 | 1,810 |

(2) frog size class (≤55 mm, 56-70 mm, and >70 mm SVL), (3) water type (pond versus river), (4) month, and (5) study site. For number of prey items and biomass indices, t-tests were used for comparisons between sexes and water types. Analysis of Variance (ANOVA) and a post-hoc Tukey's B pair-wise comparison test were used to compare frog size classes, months, and study areas. Chi-square tests were used for all diet composition comparisons. If the initial comparison between sex revealed differences, subsequent comparisons were done for each sex separately. Significance level was set at $P = 0.05$.

### Invertebrate Availability

Invertebrates were sampled using two methods (sticky trap and dip net) at the same 2-wk interval that diet samples were collected from June until late August (when wasps started consuming most of the invertebrates on the sticky traps). This time period was selected for sampling because it coincided with frog presence at the sites. Sampling occurred between the hours of 0900 and 1800, and the sequence that the six study sites were sampled was rotated to reduce bias. Placement of sticky traps and dip netting occurred where frogs would likely be feeding based on telemetry locations in a previous study (Bull and Hayes 2001)

Sticky traps were used to sample aerial invertebrates at the pond or river at each site. A sticky trap consisted of a clear four-sided plastic cover for plants that was 24 cm high and attached to a piece of white styrofoam floating on the water surface. Four pieces of clear plastic sprayed with Tanglefoot were attached on the four sides of each plant cover with velcro. These traps were collected every 2 wk, returned to the lab where invertebrates in a 10 by 10 cm square in the center of each piece were identified to order (Borror and Delong 1971), and categorized into six size classes.

Aquatic invertebrates were sampled with four sweeps of a dip net (35 by 20 cm frame and 2 mm mesh) at each pond or river stretch. Sweeps were perpendicular to the shore, 1 m in length on the substrate, ending at the shoreline, and at least 10 m from previous sweeps. Invertebrates were identified to order (Merritt and Cummins 1978), categorized into the same six size classes, and released to reduce impact on invertebrate populations.

The two methods of sampling provide a measure of the relative abundance of aerial and aquatic invertebrates, but they are not directly comparable. For invertebrates captured on sticky traps and dip nets, the number of invertebrates, the number by invertebrate size class, and the composition were compared by water type, month (June through August), and site using t-tests and ANOVA and a post-hoc Tukey's B pair-wise comparison test. The composition of orders comprising >5% of the total number of prey items was used for comparison. Because data were aggregated by day, the mean for multiple samples collected on individual days was used as the variable. The relative abundance (proportion) of invertebrates occurring in the diet and within each trap type was compared using chi-square analyses for the orders that were relatively common.

## Results

### Number of Prey Items

Between June and October, 296 diet samples were collected at the 4 study sites from 171 female and 125 male frogs. A total of 1,299 prey items were identified ($\bar{x} = 4.4 \pm 0.23$) ranging from no identifiable prey to 28 prey items per sample. No significant differences were detected in number of prey items by sex, water type, month, or site. Frogs >70 mm SVL ate significantly more prey items ($\bar{x} = 5.1$ prey items) than frogs 56-70 mm SVL ($\bar{x} = 3.8$ prey items) ($P = 0.04$).

### Diet Composition

A wide variety of prey was found in the diet samples with only three orders representing ≥10% of the composition: beetles (21%), ants/wasps (21%), and flies (10%) (Table 2). Only 14% of the prey items were in larval stages. Prey items were primarily in the smaller size classes: 40% were 1-4.5 mm in length, 29% were 5-9.5 mm, 21% were 10-14.5 mm, and 10% ≥ 15 mm (Figure 1). Composition of frog diet by order of invertebrates differed significantly by water type ($P < 0.01$) (Table 2) and among frog size classes ($P = 0.02$), but not by sex. For those 477 prey items that could be identified to family, composition of diet by family differed significantly by water type ($P < 0.01$), by sex ($P < 0.01$) and among frog size classes ($P < 0.01$). A higher proportion of stoneflies, water striders, and beetles occurred in diet samples in

TABLE 2. Number of 1,299 prey items identified to order or family that were found in diet samples of Columbia spotted frogs captured in ponds and rivers in northeastern Oregon, 2002. Prey items comprising ≤1% of the diet are not listed. Invertebrates identified to family are not included in the totals for the order.

| Phylum/Class/Order/Family | Pond | River | Total |
|---|---|---|---|
| Mollusca (mollusks) | 9 | — | 9 |
| Gastropoda (snails) | 15 | 9 | 24 |
| Arthropoda (arthropods) | | | |
| Crustacea (crustaceans) | — | 6 | 6 |
| Amphipoda (scuds) | 49 | 1 | 50 |
| Arachnida (arachnids) | — | 1 | 1 |
| Acari (mites and ticks) | 14 | — | 14 |
| Araneae (spiders) | 51 | 63 | 114 |
| Insecta (insects) | | | |
| Ephemeroptera (mayflies) | 22 | 3 | 25 |
| Odonata (dragonflies and damselflies) | 42 | 2 | 44 |
| Orthoptera (grasshoppers) | 9 | 16 | 25 |
| Hemiptera (true bugs) | 16 | 21 | 37 |
| Corixidae (water boatmen) | 8 | 7 | 15 |
| Gerridae (water striders) | 15 | 26 | 41 |
| Homoptera (aphids, scales, hoppers) | 1 | 1 | 2 |
| Aphididae (aphids) | 36 | 29 | 65 |
| Coleoptera (beetles) | 96 | 85 | 181 |
| Carabidae (ground beetles) | 18 | 43 | 61 |
| Curculionidae (snout beetles) | 3 | 12 | 15 |
| Elateridae (click beetles) | 3 | 2 | 5 |
| Hydrophilidae (water scavenger beetles) | — | 15 | 15 |
| Trichoptera (caddisflies) | 11 | 6 | 17 |
| Lepidoptera (butterflies and moths) | 33 | 23 | 56 |
| Diptera (flies) | 68 | 66 | 134 |
| Hymenoptera (ants, bees, wasps) | 9 | 9 | 18 |
| Formicidae (ants) | 99 | 52 | 151 |
| Vespidae (wasps) | 71 | 29 | 100 |
| Unknown | 35 | 24 | 59 |

rivers, and a higher proportion of scuds, mayflies, dragonflies, damselflies, backswimmers, and ants/wasps occurred in diet samples in ponds. Composition of diet differed among study sites for orders with >20 prey items ($P < 0.01$; Figure 2). Composition of diet differed over the summer among four families and 11 orders of prey items ($P < 0.01$). For the six orders with > 50 prey items found ($P < 0.01$) in diet samples, spiders, beetles, and flies decreased in abundance over the summer, and true bugs and ants/wasps increased in abundance over the summer (Figure 3).

Two recently transformed Columbia spotted frogs were found in the stomach of a female at Rainbow pond, and a Pacific treefrog (*Hyla regilla*) metamorph was found in the stomach of a female at Gun pond. These observations indicate that cannibalism occurs in this species.

## Diet Biomass

Female biomass indices were 60% larger than males (× male = 5.8; female $\bar{x} = 9.3$; $P < 0.01$), so that further analyses were separated by sex. Biomass indices of female frogs ≤55 mm SVL were significantly smaller than those in the two larger size classes (biomass index = 4.3 for frogs ≤55 mm; 10.0 for frogs 56-70 mm; 10.4 for frogs > 70 mm; $P < 0.01$). No significant differences occurred in biomass indices among the three size classes of males. By water type, males in rivers had significantly larger biomass indices ($\bar{x} = 8.1$) than males at ponds ($\bar{x} = 4.6$) ($P = 0.01$), but there were no significant differences between female biomass indices by water type. Biomass indices were significantly higher in September than in July ($P = 0.02$); no significant differences occurred in biomass indices between rivers and ponds by month or among sites.

## Invertebrate Availability

Sticky traps captured aerial invertebrates that flew or drifted into the traps, although visual observations suggest that wasps (i.e.,yellowjackets) were typically not captured and are under represented. I captured 38,583 invertebrates with the majority being flies (74%) and leaf hoppers (16%) (Table 3). Ninety-three percent of the invertebrates were 1-4.5 mm (Figure 1). No differences in number by size class or total number of invertebrates were detected between pond and river habitats. No differences were detected in total number of invertebrates among study sites. By composition (order), only leafhoppers were significantly more abundant at ponds than rivers ($P < 0.01$). By month, spiders were more abundant in July than June, and beetles and leaf hoppers were more abundant in July than August ($P < 0.01$).

I captured 4,527 invertebrates with dip nets, the majority in larval form. A considerable diversity of invertebrates was represented in the sample with the majority being snails (27%), crustaceans (16%), and mayflies (10%). By invertebrate size class, a higher percentage of these dip net samples

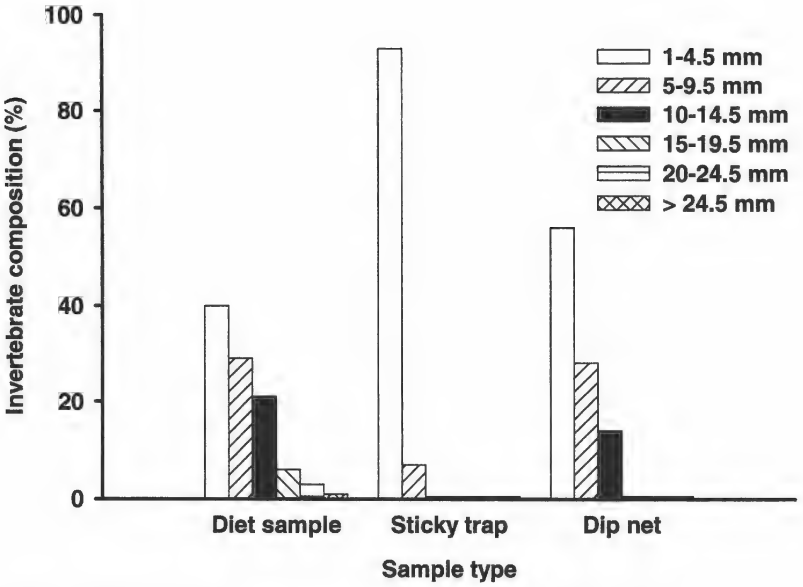


Figure 1. Proportion of invertebrates by size class consumed by frogs and captured on sticky traps and in dip net samples.

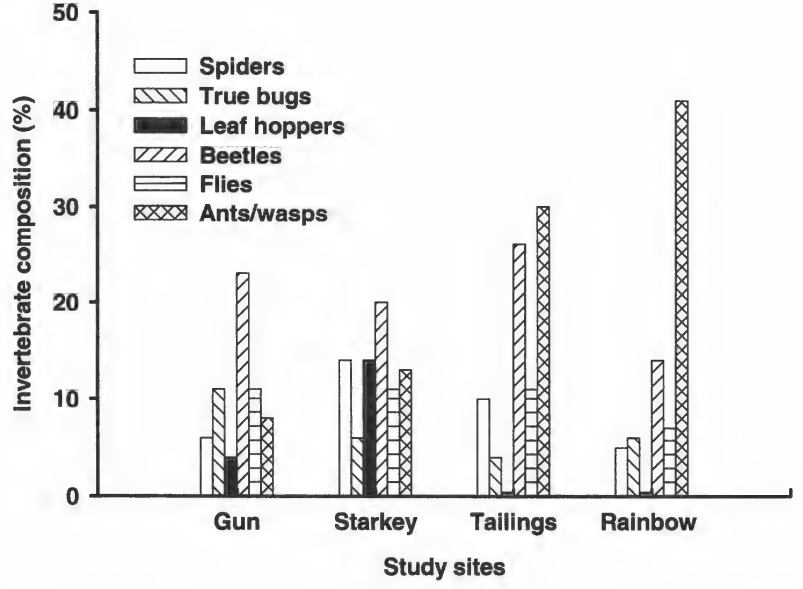


Figure 2. Proportion of invertebrates in six orders found in Columbia spotted frog diet in four study sites. Only orders with > 50 prey items are displayed.

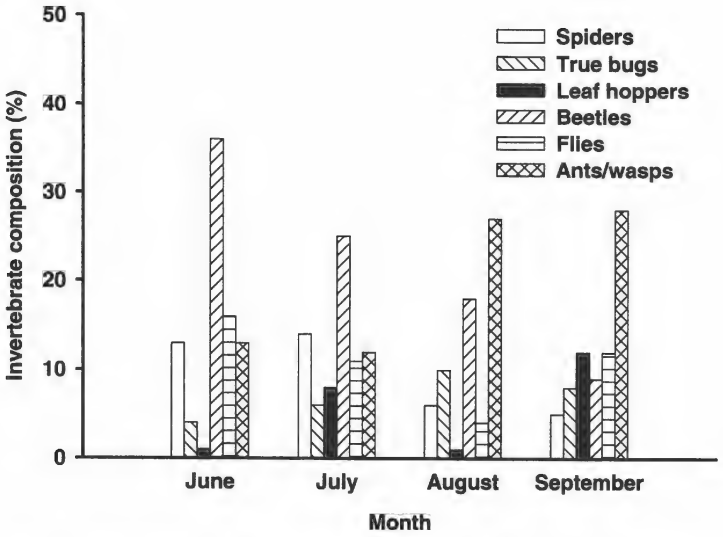


Figure 3. Proportion of invertebrates in six orders found in Columbia spotted frog diet in each of four months. Only orders with > 50 prey items are displayed.

were larger when compared to sticky traps (Figure 1). Higher numbers of all invertebrates ($P < 0.01$) and of dragonflies ($P < 0.01$), damselflies ($P < 0.01$), back swimmers ($P < 0.01$) , diving water beetles ($P = 0.03$) , leeches ($P = 0.03$), crustaceans ($P < 0.01$), and mayflies ($P < 0.01$) occurred in ponds than in rivers. No significant differences occurred in total number by size class or size class by site in ponds or in rivers. No significant differences occurred in composition by site.

Availability of invertebrates by order captured in sticky traps and dip nets differed significantly from what was found in the frog diet ($P < 0.01$; $P < 0.01$). Size class also differed between available invertebrates and those in the diet sample (sticky trap: $P < 0.01$; dip net: $P < 0.01$). Invertebrates captured on sticky traps and dip nets represented only a portion of prey available to Columbia spotted frogs. By taxonomic group, 52% and 22% of the frog diet comprised invertebrates captured in sticky traps and dip net samples. Terrestrial invertebrates (e.g., ants, beetles, larvae of butterflies and moths) and wasps made up 17% and 8% of the frog diet but were not detected with my sampling techniques.

## Discussion

Prey items found in diet samples suggested that the Columbia spotted frog is a generalist, consuming a wide variety of prey within the size range that it can catch and ingest (Table 2). Frog diet consisted of a higher percentage of larger invertebrates than was captured on sticky traps or in dip nets (Figure 1), which suggests a selection for larger prey to maximize caloric return for capture effort. It appeared that male frogs in rivers were able to obtain more biomass than males in ponds based on biomass indices, although no differences were detected in biomass obtained by females among water types.

Findings of this study concur with the great diversity of food items found in the three other quantitative studies evaluating diet of this frog species. In western Montana, 517 prey items identified in 50 stomach contents included 35% beetles, 22% ants/wasps, 14% spiders, 9% flies, 5% true bugs, 5% butterflies and moths, and <5% in other orders (Miller 1978). In central Oregon, 206 diet samples revealed representatives of 63 families in 19 orders (Whitaker et al. 1983). In Yellowstone Park in Wyoming, 70-90% of 802 prey items from178 frogs were spiders, true bugs, beetles,

TABLE 3. Percent of invertebrates in frog diet samples, on sticky traps, and in dip net samples identified to order or family that were found in Columbia spotted frog diet samples or captured in traps in ponds and rivers in northeastern Oregon, 2002. Invertebrates comprising ≤5% of the diet, sticky traps, or dip nets are not listed.

| Phylum/Class/Order/Family | Frog Diet | Sticky Trap | Dip Net |
|---|---|---|---|
| Mollusca (mollusks) | | | |
| Gastropoda (snails) | 2 | — | 27 |
| Arthropoda (arthropods) | | | |
| Crustacea (crustaceans) | | | |
| Amphipoda (scuds) | 4 | — | 16 |
| Arachnida (arachnids) | | | |
| Araneae (spiders) | 9 | 1 | <1 |
| Insecta (insects) | | | |
| Ephemeroptera (mayflies) | | | |
| Larvae | 1 | — | 10 |
| Odonata (dragonflies and damselflies) | | | |
| Larvae | 2 | — | 6 |
| Hemiptera (true bugs) | 2 | <1 | — |
| Corixidae (water boatmen) | 1 | — | 8 |
| Gerridae (water striders) | 3 | — | 4 |
| Notonectidae (backswimmers) | 1 | — | 6 |
| Homoptera (leaf hoppers) | 5 | 16 | — |
| Coleoptera (beetles) | | | |
| Adults | 9 | 1 | — |
| Larvae | 5 | — | 3 |
| Carabidae (ground beetles) | 5 | — | — |
| Trichoptera (caddisflies) | | | |
| Larvae | — | — | 7 |
| Diptera (flies) | | | |
| Adults | 10 | 74 | — |
| Hymenoptera (ants, bees, wasps) | 1 | 1 | — |
| Formicidae (ants) | 12 | — | — |
| Vespidae (wasps) | 8 | — | — |
| Total | 1,299 | 38,589 | 4,527 |

flies, and ants/wasps (Turner 1959). In Wyoming, 84% of prey items were ≤9.5 mm in length in comparison to 69% in this study. Turner (1959) suggested the peak of foraging in Wyoming was July and August with less foraging in June and September. In contrast, the greatest biomass indices occurred in September in this study. Some of these differences in prey size and temporal foraging behavior may be due to the higher elevation, colder climate, and smaller frogs found in Yellowstone Park than in northeastern Oregon.

Female frogs appeared to maximize the amount of prey they could ingest because of the need to produce eggs annually. Females >55 mm SVL had larger diet samples than males of the same size, while females ≤55 mm SVL consumed less prey than males of the same size. These smaller females will probably not be reproductive the following year (Licht 1975), so that there may not have been the energy needed for egg production.

Our findings suggest that frogs foraged actively from June through September and into October at the Gun and Rainbow sites with greater biomass indices in September than in July. It is likely that active foraging occurred prior to June, although diet samples were not collected then. These observations suggest frogs were maximizing their foraging late in the season, presumably for overwintering, or for egg production in the case of females. The differences in composition of diet by month may well reflect relative availability of invertebrates at different times during the summer (Figure 2). Spiders and leafhoppers were most abundant in July on both sticky traps and in diet samples. Beetles were most abundant in June in the diet but in July on sticky traps.

Differences in diet among study sites were observed in this study (Figure 2) and Whitaker et al. (1983). They suggested that past management practices, particularly livestock grazing, contributed to differences in diet. The Starkey site was the only one with livestock grazing in our study, and this site had a more even distribution among the primary orders used for prey than the other study sites. An obvious difference among the study sites was the high percentages of wasps at Tailings and Rainbow, the two sites with the highest elevations. Either these sites had a higher density of wasps than the other sites or a lower density of other prey. Wasps were able to escape from sticky traps, so that relative availability of this prey item can not be determined among the sites.

The results of sampling available invertebrates suggest that ponds provided more aquatic invertebrates, but abundance of aerial invertebrates was fairly even between ponds and rivers. In spite of this presumably greater prey base in ponds, diet samples of males had greater biomass on rivers, which may be a primary reason frogs inhabited rivers over ponds (Bull and Hayes 2001). Additional factors that could enter into the selection of habitat include predation and water temperature, as it relates to metabolic rate. Research comparing kinds and rates of predation and water

temperatures between ponds and rivers would be informative and may shed some light on the declines of this species within portions of its range.

## Acknowledgements

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## Literature Cited

Borror, D. J., and D. M. Delong. 1971. An Introduction to the Study of Insects. Third edition. Holt, Rinehart and Winston, New York.

Bull, E. L., and M. P. Hayes. 2001. Post-breeding season movements of Columbia spotted frogs (*Rana luteiventris*) in northeastern Oregon. Western North American Naturalist 61:119-123.

Bull, E. L., and M. P. Hayes. 2002. Overwintering of Columbia spotted frogs in northeastern Oregon. Northwest Science 76:141-147.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. United States Department of the Interior, Fish and Wildlife Service, Office of Biological Services, Washington, D.C.

Hovingh, P. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. Great Basin Naturalist 53:168-179.

Legler, J. M., and L. J. Sullivan. 1979. The application of stomach-flushing to lizards and anurans. Herpetologica 35:107-110.

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Licht, L. E. 1975. Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations. Canadian Journal of Zoology 53:1254-1257.

Merritt, R. W., and K. W. Cummins (editors). 1978. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company.

Miller, J. D. 1978. Observations on the diets of *Rana pretiosa*, *Rana pipiens*, and *Bufo boreas* from western Montana. Northwest Science 52:243-249.

Morell, V. 1999. Are pathogens felling frogs? Science 284:728-731.

Patla, D. A., and C. R. Peterson. 1999. Are amphibians declining in Yellowstone National Park? Yellowstone Science 1999:2-11.

Reaser, J. K. 2000. Demographic analysis of the Columbia spotted frog (*Rana luteiventris*): case study in spatiotemporal variation. Canadian Journal of Zoology 78:1158-1167.

Turner, R. B. 1959. An analysis of the feeding habits of *Rana p. pretiosa* in Yellowstone Park, Wyoming. American Midland Naturalist 61:403-413.

Whitaker, J. O., Jr., S. P. Cross, J. M. Skovlin, and C. Maser. 1983. Food habits of the spotted frog (*Rana pretiosa*) from managed sites in Grant County, Oregon. Northwest Science 57:147-154.

# Northwest Science Notes

*The purpose of Notes is to publish papers typically less than five pages long. No specific format or content is required for articles published as Notes, but all will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.*

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## Observations on the Nesting Distribution of Great Blue Herons on the Hanford Reach of the Columbia River

### Introduction

The Hanford Reach is an 80-km segment of the Columbia River extending downstream from Priest Rapids Dam to near Richland in southcentral Washington (Figure 1). This segment differs from the rest of the river upstream from tidewater because it is not impounded by a dam (Geist 1995). Here most of the river flows through federal property (Hanford Site) but the eastern shore downstream from Savage Island is private (Figure 1). Land use on the Hanford Site differs from surrounding landscapes because towns and irrigated fields have been abandoned since 1944. Public access to the river shore has been restricted because of the presence of nine plutonium production reactors at six separate locations along the western rivershore (Figure 1). Since 1944, the Hanford Site has served as a refugium for native plants and wildlife in a larger surrounding region devoted to cultivation agriculture and urbanization (Gray and Rickard 1989). The purpose of this note is to summarize observations concerning the distribution of great blue herons (*Ardea herodias*) along the Hanford Reach. This is important because it provides some insight as to the ability of great blue herons to adapt to an environment changing in response to the activities of people.

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### Methods

Information concerning the distribution of heron nests along the Reach was obtained from published literature and personal observations since the 1970s. In the years 1994 to 2001 counts of active nests were made by visiting colonies all along the reach in July and August when the active nests were identified by the presence of preflight nestlings. Because road access to the shoreline is limited the colonies were accessed by boat.

### Results

In 1950 twelve great blue heron (*Ardea herodias*), nests were placed in two mulberry trees (*Morus alba*), on Locke Island (Figure 1). At that time these were the only great blue heron nests on the Reach (Hanson 1968).

Most of the heron nests on the Reach since 1950 have been placed in trees planted at now abandoned farmhouses near the river shore in the early 1900s (Figure 1). These trees, mostly black locust (*Robinia pseudo-acacia*), and Siberian elm (*Ulmus pumila*), have survived in this dry climate (16 cm annually) in the absence of irrigation water because they have root access to a water table <10 m below the ground surface (Rickard and Price 1989). These trees are senescent and vulnerable to wildfire, windfall and insect infestation. Their future is limited. Many recently selfestablished native and alien trees now grow



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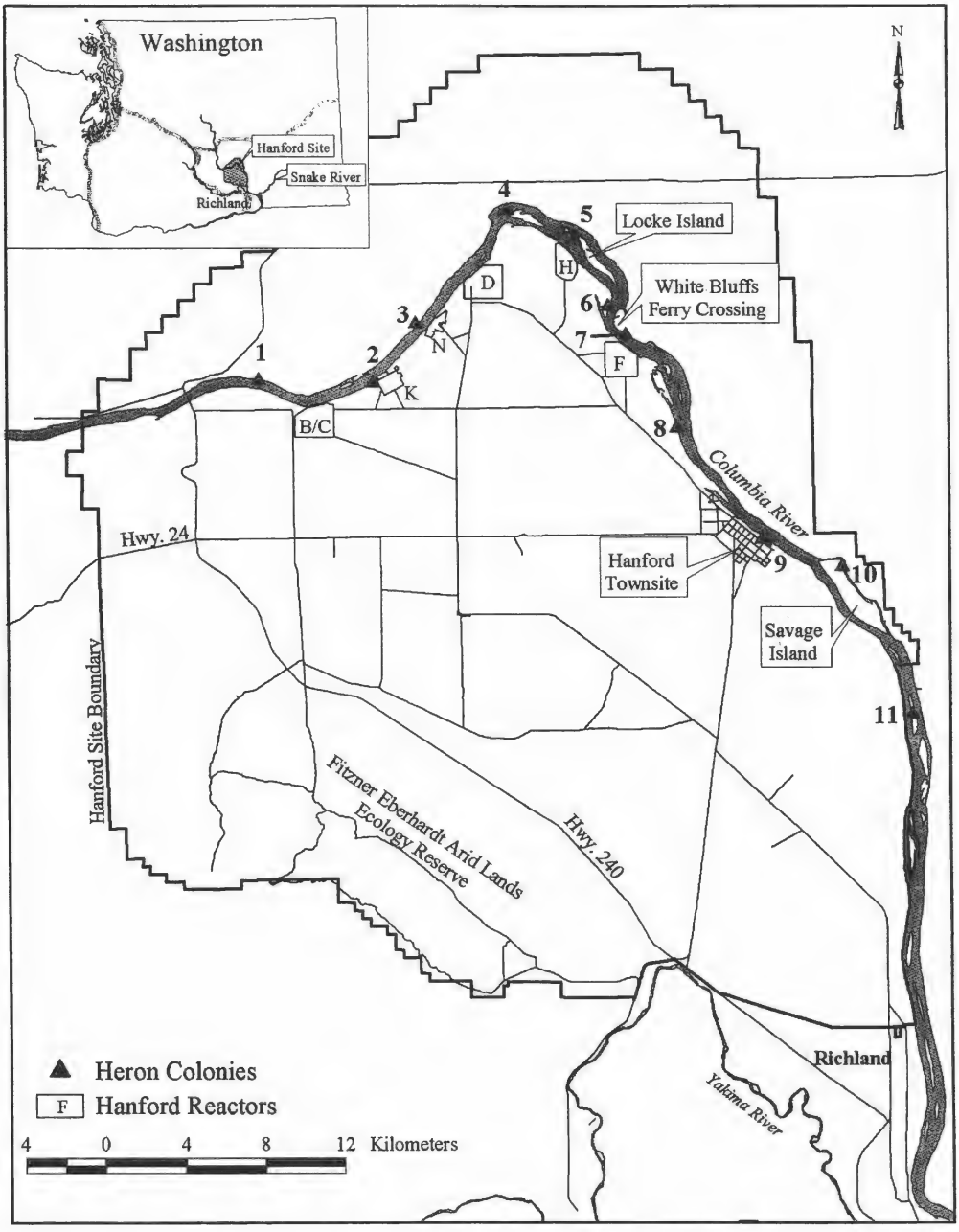


Figure 1. Map of the Hanford Reach of the Columbia River, showing the distribution of heron colonies.

on riverine beaches that historically were devoid of trees (Snodgrass 1904). The spread of these self established trees is apparently encouraged by the diurnally fluctuating river flow regulated by upriver hydroelectric dams (Rickard and Poole 1989). These newly established trees may provide heron nest sites in the future but observations show that only self-established trees on island shores have been selected as nesting sites. No heron nests have been placed in shoreline trees planted on private land.

The number of active great blue heron nests along the Reach has declined from 75 to 34 since 1994 (Table 1). The decline has occurred at 6 of the 11 colonies monitored between 1994 and 2001. The greatest number of nesting great blue herons occurred at Colony 7, however, total nests observed there each year also steadily declined throughout the 1990s. The cause(s) of the decline at colony 7 are not known, but they are not likely related to a decline in fledging success (Marco 1997). Interspecific competition for suitable nesting sites was also not likely related to great blue heron nest declines at colony 7 because no other piscivorous avian species such as the black-crowned night heron (*Nycticorax nycticorax*), double-crested cormorant (*Phalacrocorax auritus*), or great egret (*Casmerodius albus*), have nested there. Vehicle, pedestrian, and boat traffic occur regularly during the nesting season near colony 7. Great blue heron nests at colony 10 declined from 16 pairs in 1994 to 6 in 1995 and 1996, and 7 in 1999. This decline coincided with the loss of a few trees at this colony caused by a wild fire during the summer of 1994. Heron nests at the island colony 11 were located in a tall, steel transmission line tower (Table 1). In 1994 there were 16 active nests in the tower and 12 in 1995 (Table 1). In 1996 a red-tailed hawk (*Buteo jamaicensis*) nested in the tower and there were no active heron nests in 1998, 1999, and 2001. Colony 6 was used until 1998 when a pair of bald eagles (*Haliaeetus leucocephalus)* began nesting there. Since then, there have been no active heron nests at this site. A nest tree at heron colony 8 that historically contained more than 20 nests toppled after 1990. To date no herons have nested in the surviving trees there. The number of great blue herons nesting at colonies 2 and 9 appear to have increased between 1994 and 2001. Public access to these colony sites is limited to boat traffic only.

Table 1. Number of active great blue heron nests at colonies along the Hanford Reach of the Columbia River 1994, 1995, 1998, 1999, and 2001

| Colony | 1994 | 1995 | 1998 | 1999 | 2001 |
|---|---|---|---|---|---|
| 1 | | 3 | | | |
| 2 | | | | 1 | 5 |
| 3 | 5 | | | | 1 |
| 4 | 2 | 5 | | | 1 |
| 5 | | 5 | 2 | 1 | 1 |
| 6 | 9 | 6 | 8 | | |
| 7 | 31 | 30 | 25 | 23 | 21 |
| 8 | | | | | |
| 9 | 3 | 2 | 2 | | 5 |
| 10 | 16 | 6 | 6 | 7 | |
| 11 | 16 | 12 | | | |
| Total | 75 | 69 | 45 | 37 | 34 |

## Discussion

The general decline in great blue heron nests found along the Hanford Reach of the Columbia River is not likely from reduced fledging success at the colonies there. The general decline in large trees found along the Columbia river where public access is restricted during the breeding period may be the most limiting physical characteristics for great blue heron nesting habitat there. The two colonies that have been established on telephone-line towers support the premise that natural colony trees were limiting resources. The observations also suggest these man-made structures can supplement nesting habitat for great blue herons, but competition for nesting sites with raptors may be an issue. Low sub-adult or adult survival and immigration rates may also be limiting factors for nesting great blue herons along the Hanford Reach of the Columbia River. During the mid-1990s many tags from juveniles and adults were returned to PNNL researchers by staff of the Wildlife Services Division of the United States Department of Agriculture. Legal shooting of the sub-adult and adult great blue herons at the nearby Ringold hatchery supports the premise that this source of mortality may have contributed to the observed population decline of great blue herons along the Hanford Reach of the Columbia River.

## Acknowledgements

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## Literature Cited

Geist, D. R. 1995. The Hanford Reach: What do we stand to lose? Illahe 11:130-141.

Gray, R. H. and W. H. Rickard. 1989. The protected area of Hanford as a refugium for native plants and animals. Environmental Conservation 16:251-260.

Hanson, W. C. 1968. Recent history of double-crested cormorant colonies in southeastern Washington. The Murrelet 49:25-26.

Marco, J. D. 1997. Factors affecting great blue heron reproduction in southcentral Washington. M.S. Thesis, University of Idaho, Moscow, Idaho.

Rickard, W. H. and L. D. Poole. 1989. Terrestrial wildlife of the Hanford Site: Past and future. Northwest Science 63:183-193.

Rickard, W. H. and K. R. Price. 1989. Tritium uptake from groundwater by black locust trees. Northwest Science 63:87-89.

Snodgrass, R. E. 1904. A list of land birds from central and southeastern Washington. The Auk 21:223-233.

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*Accepted for publication 14 July 2003*

## Book Review

### Wildlife-Habitat Relationships in Oregon and Washington

David H. Johnson and Thomas A. O'Neil (managing directors). 2001. Oregon State University Press. 736 pages. ISBN 0-87001-488-0. Hardcover, $65.00.

To start with, this is an impressive effort, consisting of over 700 pages divided into 27 chapters, with an accompanying CD-ROM of digital data. The project involved a tremendous number of people (88 chapter authors alone!) and presented a wide variety of information on wildlife and habitat of Oregon and Washington. As such, it is a large book and is not for the casual reader! The main objective of the work, as stated by the managing directors in the preface, is to synthesize and disseminate current state of knowledge about the wildlife resources in Washington and Oregon. To that end, the managing directors did a good job in organizing the chapters in a reasonable sequence. All of the chapters present relevant information on wildlife-habitat issues facing Oregon and Washington.

The initial six chapters presented the core of the theme for the book, defining terms, habitat, and conservation issues. It is of interest to note the extensive treatment in Chapter 1 on defining "wildlife habitat type" or "habitat type"; it reflects one of the problems we face in science—semantics! The next nine chapters (7–15) treat wildlife complexes in the various habitats found in Washington and Oregon. Again, the treatment is extensive and, as stated in the preface, "...will be used in natural resource planning, conservation, and education efforts for years to come." The next four chapters (16–19) deal with more specific wildlife issues such as introduced species (chapter 16), genetic considerations (chapter 17), and species at risk (chapter 19). Again, each of these themes is extremely relevant regarding wildlife-habitat relationships and each provides sufficient treatments of the topics. Chapter 20, which deals with how one puts all this information together, provides a brief but good link to the two chapters on models and their application to resource issues. Chapter 23 is an in-depth treatment of how we would apply defined goals to management, in this case, forest management. The next three chapters concern specific subjects: decaying wood as a resource (chapter 24), single vs. multiple species management (chapter 25), and salmon (chapter 26). The last chapter is an introduction to the CD-ROM, which does indeed provide the reader access to valuable and extensive databases of information.

Overall, the material in this book was well presented and will provide the valued resource that the managing editors had hoped for. However, there are a few detracting aspects of the book that need to be addressed.

In chapter 2, color photographs at the lead of each habitat type would have helped, although the authors did provide some color examples in the back. Also, small maps indicating locations of these habitats would have been useful. In chapter 3, the authors used the classic succession-climax paradigm, which I consider a bit archaic, especially in reference to grass-shrub communities. I found interesting the comment that fires, often a natural event, were mimicking clearcuts, an anthropogenic event! Also, I could not find Table 2 (page 137). In chapter 4, the use of the old carrying capacity paradigm does not reflect the more current dynamic view of populations. Chapter 6 seemed to be a little heavy in ecological acronyms, but they likely are needed to keep everything straight.

The treatments in chapters 7–15, in general, seemed biased toward Oregon; often only maps of Oregon were supplied. It is unclear if that reflects an imbalance of available information or not. A map at the beginning of each chapter to show location and extension of each habitat would have been helpful. Although each chapter was authored by different—often several—persons, so that style and content vary, these chapters could have benefited from a more coordinated presentation.

A lack of figure numbers and legends in chapter 18 made it difficult to coordinate the figures with the text. Although this chapter contained a good,



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detailed description of the topic, a final conclusion section would have been in order.

I found the use of numbers for references to be distracting, making it hard to judge how current information was without referring to the end of the chapters. Also, although a central idea of the book was to consider Oregon and Washington as a single regional unit, rarely did maps or images present both states together. I felt the presentations tended to be biased toward Oregon, as well as toward western forest habitats rather than the more extensive shrub and grasslands. Missing too was a detailed treatment of fires other than discussions that were interspersed through various chapters.

Apart from these minor distractions, however, I believe the managing directors and the hundreds of persons who participated in *Wildlife-Habitt Relationships in Oregon and Washington* did achieve their stated goal. They have indeed, presented the states of Washington and Oregon with valuable resource material, that can no doubt contribute to the wise management of the wildlife resources in these two states.

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# NORTHWEST SCIENCE

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The purpose of Notes is to publish papers typically less than five journal pages long. Suggested topics include preliminary results, new methods, significant range extensions, and perhaps taxonomic observations. There is no specific format or content required for Notes, but all will be peer-reviewed and must be scientifically creditable. Authors may contact the Editor about the suitability of manuscripts to be published as Notes.

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This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum may not be peer-reviewed so that publication is expedited. The Editor reserves the right to edit manuscripts for clarity and conventions of standard written English.

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Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten in 12 point Times New Roman font, on 8.5" x 11" paper, double-spaced throughout (including Abstract, Acknowledgements, Literature Cited, Tables, and Figure captions). Use the front of the page only. Allow one-inch margins around the page. The format and style of manuscripts should conform to general usage in recent issues, and should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgements)
- Literature Cited
- Footnotes
- Tables
- Figure Captions
- Figures

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In that situation, lowercase letters will be used. Do not hyphenate words at the ends of lines. Words to be italicized will be typed in italic rather than underlined.

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The first page of the manuscript should contain:

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Start the text on the third page, and use continuous pagination. Do not start new sections on new pages.

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  ...studied by Smith and Brown (1999)...

  ...studied by Smith et al. (2000)...(if more than two authors in a citation)

- Format B:

  ...was previously investigated (Smith 1991, Jones 1995, Harris 2000)

  ...results of other investigations (Smith 1991, 1995; Jones 1993; Brown 1999)

Numbers from one to nine will be spelled out, while Arabic numerals will be used for numbers 10 and larger. Exceptions to this convention are: 1) a series of mixed numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 5 g, 0.7 mm, 3 $m^2$). Arabic numerals will also be used for dates, times, page numbers, and percentages.

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Double-check literature to ensure that citations in the text and in Literature Cited agree. On one submitted copy, indicate by green check marks on each citation in the text and each citation in Literature Cited that the references have been double-checked.

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Cêska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.

Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

### *Monographs or books*

Edmunds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest Health and Protection. McGraw-Hill, New York. *(number of pages unnecessary)*

Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.

Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

### *Papers in proceedings or symposia*

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pages 363-393 *In* H. Barnes (editor), Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, UK.

Madany, M. H. and N. E. West. 1980. Fire history of two montane forest areas of Zion National Park. Pages 50-56 *In* M. A. Stokes and J. H. Dieterich (technical coordinators), Proceedings—Fire History Workshop. USDA Forest Service General Technical Report RM-81. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.

### *Theses, dissertations, and articles in press*

Donald, D. B. 1971. The limnology of the plankton of three temporary ponds in Alberta. M.S. Thesis, University of Calgary, Calgary, Alberta.

Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. Ph.D. Dissertation, University of Utah, Salt Lake City, Utah.

Dunwiddie, P. W. *In Press.* Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science. *(if the publication date is unknown or uncertain)*

Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. Ecological Applications 10: *(in press). (if the publication date is known and certain).*

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Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho.

Washington Agricultural Experiment Station Technical Bulletin Number 60. Washington State University.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

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USDA Forest Service. 1998. Fire effects information system. Prescribed Fire and Fire Effects Research Work Unit, Rocky Mountain Research Station, Missoula, Montana. Available online at www.fs.fed.us/database/feis/

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